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Nitrification and Denitrification in the Eastern Tropical North Pacific

By

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Introduction

The eastern parts of the tropical oceans are generally more productive than the central or western parts (HENTSCHEL, 1936), due to "upwelling" or other processes which bring up nutrient rich water from below into the upper lighted zone. Associated with a high production in the upper zone there is a strong oxygen depletion below the photosynthetic layer, brought about by the remineralization of sinking organic material. Such depletion of oxygen is accentuated in areas where there are both a highly productive, photosynthetic layer and a strong thermocline which impedes convection and exchange of water richer in oxygen from above. WATTENBERG (1938) reported 0·37 ml/l as the lowest oxygen value in the oxygen minimum layer off South-West Africa during the "Meteor" Expedition.

Due to the weaker circulation in the Pacific Ocean we find that the oxygen concentration is considerably smaller than that observed in the Atlantic. In the Eastern Tropical Pacific, off the American coasts between 8°N and 21°N, a very large body of water is found of which the oxygen content is almost zero (SVERDRUP, JOHNSON and FLEMING, 1942 (Fig. 207); WOOSTER and CROMWELL, 1958).

Such anaerobic conditions, unusual for open waters, have far-reaching effects on animals inhabiting the oxygen minimum layer (KANWISHER and EBELING, 1957). It is also profitable to examine the relations between oxygen and nitrite concentration in order to obtain some information on the decay processes of organic matter under anaerobic conditions.

The Nitrogen Cycle

BRANDT's and RABEN's work first showed the value of chemical investigations to elucidate planktological studies, and since then measurements of phosphate, and sometimes nitrate, have become gradually routine observations in the oceanographic research. It has been held by BRANDT (1899, 1902) and others

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that the cycle of nitrogen in the sea follows essentially the same steps as observed in the soil by earlier investigators.

VON BRAND and RAKESTRAW were able to demonstrate *in vitro* the three steps of nitrogen oxidation associated with the decay of marine plankton: ammonia, nitrite, and nitrate, in their classical experiments published in the years 1937–1942.

After death of plankton organisms ammonia is liberated from organic compounds by the activity of bacteria. Most of heterotrophic bacteria take part in this ammonification of nitrogenous, organic matter. The process is largely the result of deamination which occurs when proteins or the products of their hydrolysis are used as energy sources (HUTCHINSON, 1957). Additionally, some ammonia is discharged directly into the water as excretory product from animals or formed by prior breakdown of urea or uric acid.

In the presence of oxygen ammonia is converted into nitrite by the agency of autotrophic organisms, some of which are *Nitrosomas* and *Nitrosococcus*. They may live in the absence of organic matter, obtaining their carbon through assimilation of carbon dioxide and their energy to carry on life processes through oxidation of ammonia to nitrite. These forms do not occur freely suspended in the open ocean but are attached to plankton organisms. Sinking and dying plankton often accumulates in the thermocline, due to rapid increase of viscosity and density. Thus many investigators found a nitrite peak associated with the thermocline layer (RAKESTRAW, 1936; GILSON, 1937).

Continuing the nitrification, other bacteria oxidize nitrite to nitrate. These organisms are difficult to detect, however, *Nitrobacter*-like forms have been found in the sea (ZOBELL, 1946).

HARVEY (1926), and especially COOPER (1937), followed the seasonal variations of the components, ammonia, nitrite, and nitrate, in the English Channel, proving their succesive occurrence in the sea after a plankton outburst in spring. RAKESTRAW (1936) and WATTENBERG (1937) pointed out that the consideration of the nitrite concentration in the water is especially useful because of its intermediate position between ammonia and nitrate, and that it might be a possible indicator of the state of equilibrium between the oxidation and reduction processes making up the nitrogen cycle.

Although the methods for determining nitrite are very simple and accurate, there are only few data available. This is especially true for tropical regions, from where there are only those reported by RAKESTRAW (1936) in the Caribbean Sea, those collected by WATTENBERG (1937) off the coast of North-West Africa, and by GILSON (1937) in the Indian Ocean.

Methods and Collection of Data

The present paper includes results which were obtained in the Eastern Tropical Pacific on SCOPE Expedition during 7. November to 17. December 1956, and data from selected stations occupied during ISLAND CURRENT Survey from 8. May to 12. June 1957. SCOPE Expedition was initiated by the Scripps Institution of Oceanography and the ISLAND CURRENT Survey by the Inter-American Tropical Tuna Commission. The main efforts of both expeditions were concentrated on plankton work, measurements of primary production, and of the current system. There was, however, opportunity for the author to carry out a number of additional chemical analyses at selected

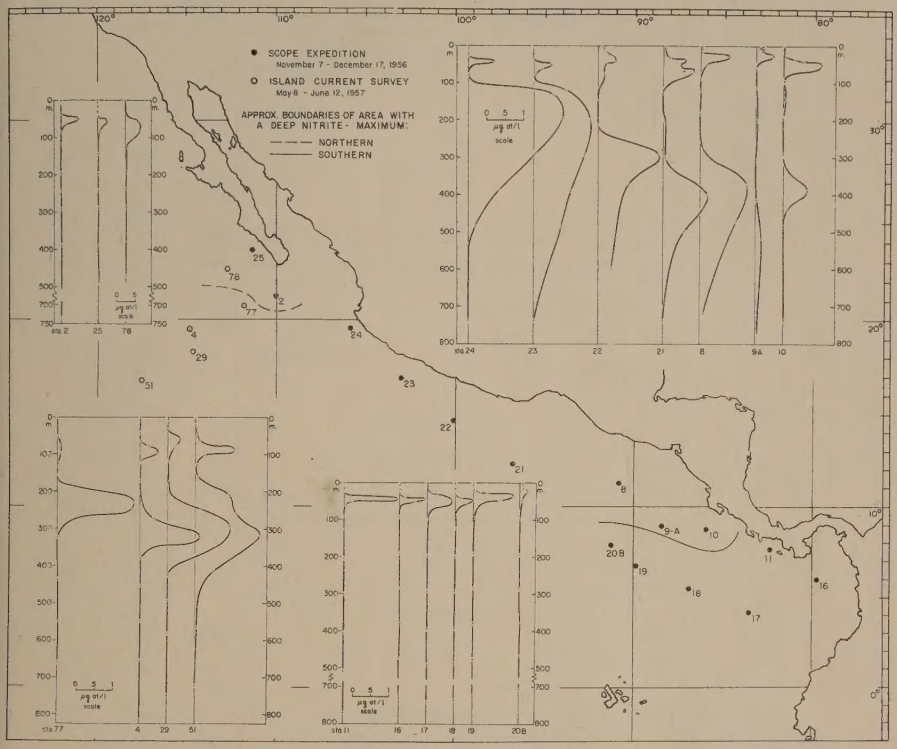

Figure 1. Nitrite occurrence in the Eastern Tropical North Pacific with indication of area with a deep nitrite maximum. Positions and nitrite curves of stations occupied during SCOPE Expedition, 1956 and ISLAND CURRENT Survey, 1957.

stations. In this paper special attention is paid to the distribution of nitrite. Table 1, at the end of this paper, summarizes the measurements used in this study. Complete data of all stations occupied on SCOPE Expedition are reported in HOLMES (1958).

Nitrite measurements were made with a Beckman DU Spectrophotometer, employing the method of BENDSCHNEIDER and ROBINSON (1952), and using a 10 cm cell. The values are reported in μg at. N/l with an accuracy of about 5%.

Measurements of dissolved oxygen were made as a matter of routine, using the Winkler technique according to the direction of WOOSTER (1950). The procedure was to introduce 2 ml of $MnCl_2$ solution and 2 ml of KOH-KI solution into a 250 ml bottle. After adding the reagents, the bottle was well shaken and the acid added after precipitation, then titrated in the usual way. The values are reported in ml/l oxygen.

Off the Mexican and Central American coasts the oxygen content of the water below the thermocline is extremely low, and the error caused by oxygen introduced with the reagents may be of high percentage. OHLE (1953) found

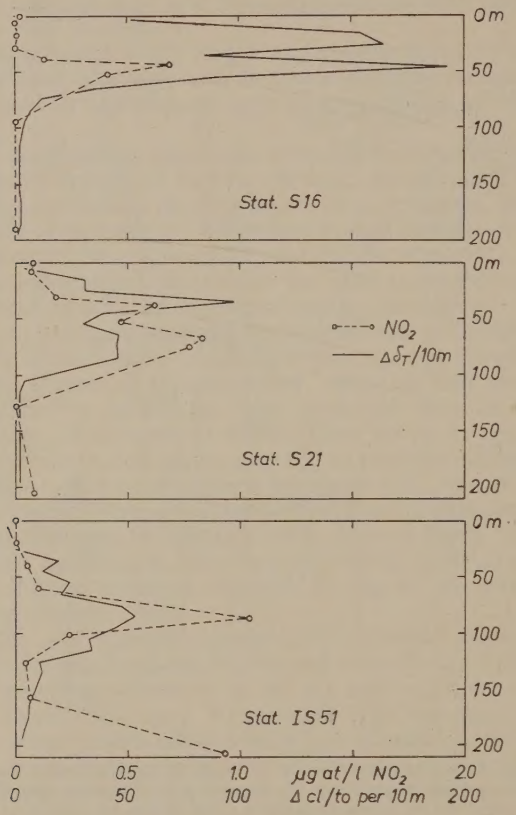

Figure 2. Relationship between stability (full line) and nitrite concentration (broken line). Stability is expressed as the difference in thermosteric anomaly (centilitres per ton) for a water column of 10 m. Nitrite in µg at. N/l. For positions of stations see Figure 1. SCOPE Expedition (S), 1956 and ISLAND CURRENT Survey (IS), 1957.

for both manganous chloride and potassium hydroxide solutions of similar concentrations as used on the cruises, an oxygen content of about 0·007 mg/ml = 0·005 ml/ml, which was constant over a rather long storing period. If we assume that the reagents, used on the expeditions, hold approximately the same oxygen concentration (it might be somewhat less since OHLE worked in temperate climate) we introduce 0·02 ml oxygen into a 250 ml bottle. This would be an error of 0·08 ml/l. In the oxygen poor area, described by SVERDRUP, we find values of this magnitude, when using the shipboard routine procedure. The oxygen content is probably zero in such cases.

Another error could be caused by the oxidation or reduction of the iodide ion to elementary iodine, or vice versa by reagents in the sea water, e. g., the oxidizing action of nitrite which would also result in a higher value:

$$2\ HNO_2 + 2\ HCl + 2\ KI = I_2 + 2\ NO + 2\ KCl + 2\ H_2O.$$

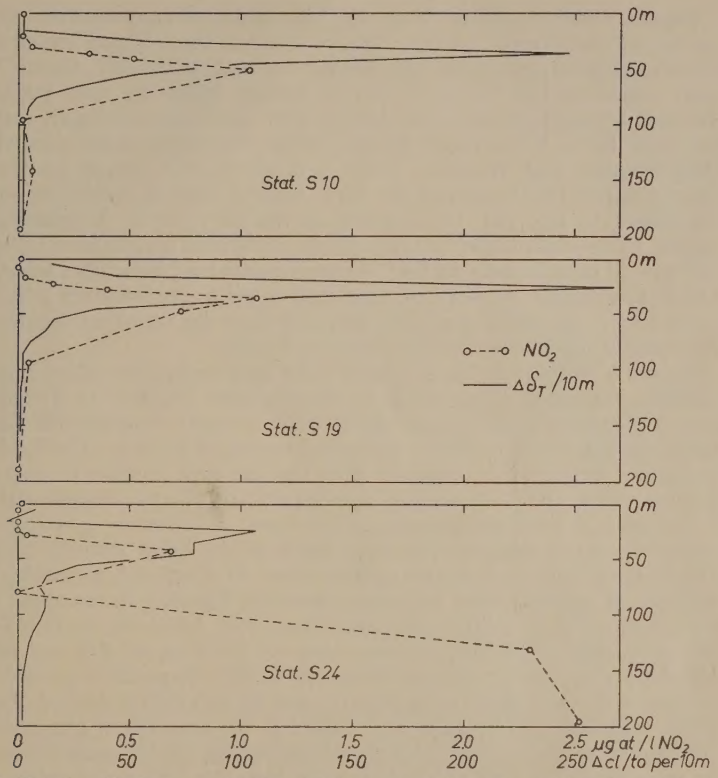

Figure 3. Relationship between stability (full line) and nitrite concentration (broken line). Stability is expressed as the difference in thermosteric anomaly (centilitres per ton) for a water column of 10 m. Nitrite in μg at. N/l. For positions of stations see Figure 1. SCOPE Expedition (S), 1956 and ISLAND CURRENT Survey (IS), 1957).

This amount, however, is negligible, since the highest nitrite values encountered in the region are only 2·5 μg at. N/l.

Iodate measurements, recently carried out by SUGAWARA (unpubl. report) in the Central Pacific, show that one has possibly to consider this chemically as well. To avoid all these errors it is suggested that OHLE's (1953) Iodine-difference-method should be used.

Results

1. Nitrification

In the Eastern Tropical Pacific conditions are specially favourable for a strong decay of planktonic material. Figure 1 reveals that in close association with the thermocline a nitrite maximum exists within the upper 100 m all over the region investigated. In both seasons, summer and winter, this maximum is more or less obvious, not only in the region with a high production but, surprisingly, also in the north-western part which is normally very barren (BRANDHORST, 1958).

Figures 2 and 3 confirm the strong relationship between the occurrence of nitrite and the density gradient. Figure 2 shows three typical examples of a nitrite maximum coinciding with the layer of highest stability. Figure 3 represents cases in which the nitrite peak is located below the most stable layer. The stability is expressed as the difference in thermosteric anomaly (centilitres per ton) for a 10 m water column. Since the thermosteric anomaly (δT) (MONTGOMERY and WOOSTER, 1954) is in use at the Scripps Institution of Oceanography for computing the mass field in tropical waters, it was most convenient to represent the stability in the above term. Temperature and salinity curves were drawn for each station on special graph paper from which $\Delta\delta$T per 10 m was easily read off. Additionally to the Nansen bottle lowerings, bathythermograph observations were used to get a more detailed temperature curve for interpolation between points obtained by reversing thermometers. Positions of the stations used are given in Figure 1.

Station S 16 (Fig. 2), located in the Gulf of Panama, shows two significant stability maxima, an upper one at 25 m and a lower one at 45 m. This distribution of thermosteric anomaly is due to water of very low salinity (28 $^0/_{00}$) overlaying the thermocline, which is sharpest at about 45 m. In the Gulf of Panama low saline surface water originates from the very high rainfalls in summer and autumn. Below 100 m the stability is rather low and almost constant with depth.

The peak of the corresponding nitrite curve, indicated by a broken line, is rather sharp and occupies the same depth as the lower stability maximum. There are not many observation points below 50 m and it is probable that the decrease of nitrite is more rapid than drawn in Figure 2. In the upper stablity maximum at 25 m, nitrite values are almost zero. Near this depth (18 m) the lowest phosphate content has been observed (0·18 μg at. P/l) and nitrate is especially low between 18 and 29 m. On SCOPE Expedition routine nitrate analyses were carried out using MULLIN and RILEY's (1955) method. However, as the values are too irregular with regard to the amounts of phosphate, they are considered not accurate enough. At this station only traces of nitrate could be detected in 18 and 29 m, whereas water from the surface and below 39 m is very high in nitrate (1–3 μg at. N/l). This suggests the possibility that phytoplankton may have used the nutrients in the upper stability maximum, if light conditions would have been sufficient. The lower stability maximum may be situated below the depth of sufficient illumination and as a result of the decay of accumulated plankton, nitrite appears here. Unfortunately the depth intervals of chlorophyll "*a*" measurements were too widely spaced as to be of use for this interpretation. The chlorophyll "*a*" content for the upper 50 m averaged about 0·3–0·4 mg/m^3, which is considered a moderate value for this area.

Station S 21, 250 miles south-west of the Gulf of Tehuantepec, has a similar character with regard to a double stability maximum. A very pronounced upper maximum is observed at about 35 m, a less distinct one between 65 and 85 m. In this case each stability maximum is accompanied by a nitrite peak, which indicates to some degree that the above consideration may be right, and that here the plankton, accumulated in the upper stability maximum at 35 m, may be unable to use all the nitrite produced, since light conditions may be insufficient at this depth. The chlorophyll "*a*" content down to 25 m is about 0·9 mg/m^3; at 50 m 1·4 mg/m^3.

Station IS 51, far offshore in 16°50′N and 117°30′W, has one stability maximum at 85 m, which coincides with a nitrite peak. In the upper 20 m

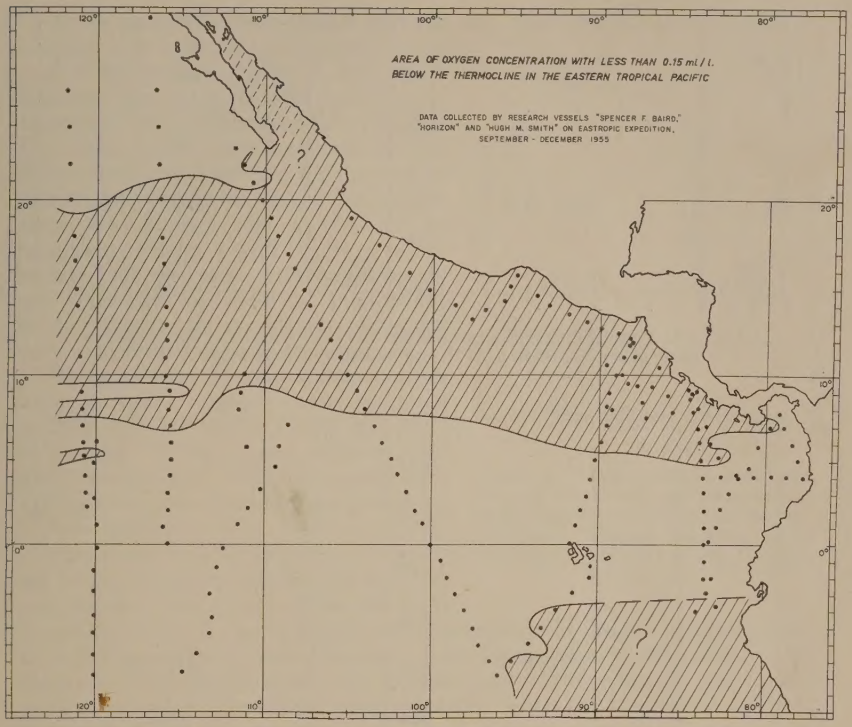

Figure 4. Area of oxygen concentration (hatched) with less than 0·15 ml/l below the thermocline in the Eastern Tropical Pacific. EASTROPIC Expedition, 1955.

there is a slight instability. The rise of the nitrite content at 200 m is due to reduction processes, which will be treated later on.

The next series in Figure 3 represents curves of those stations where the nitrite peak is located below the stability maximum. At stations S 19, S 24, and S 10 the thermocline is quite shallow (25 and 35 m respectively) and it seems to be probable that plankton, if accumulated in this layer, should obtain enough light for assimilation, and be able to use nitrite from the upper level, resulting in a lowering of the nitrite peak for 10 to 20 m.

2. Denitrification

Many species of denitrifying bacteria exist in the sea (ZOBELL, 1946), some of which are able to reduce nitrate to nitrite under anaerobic or nearly anaerobic conditions in the presence of abundant organic matter. In this process the oxygen of nitrate is used in the oxidation of organic matter without the direct utilization of molecular oxygen present in the sea water.

In the oxygen depleted region off the west coasts of America, it is possible to see whether the reduction processes, often observed in shallow coastal waters and lakes, also occur in the open sea. Figure 4 shows the horizontal extension

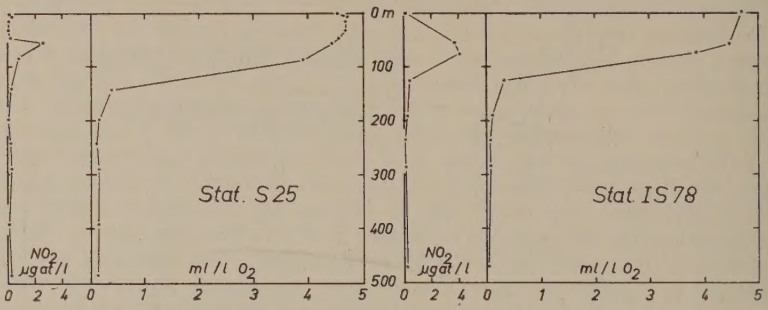

Figure 5. Vertical distribution of oxygen and nitrite north of the reduction zone. SCOPE Expedition, 1956 and ISLAND CURRENT Survey, 1957.

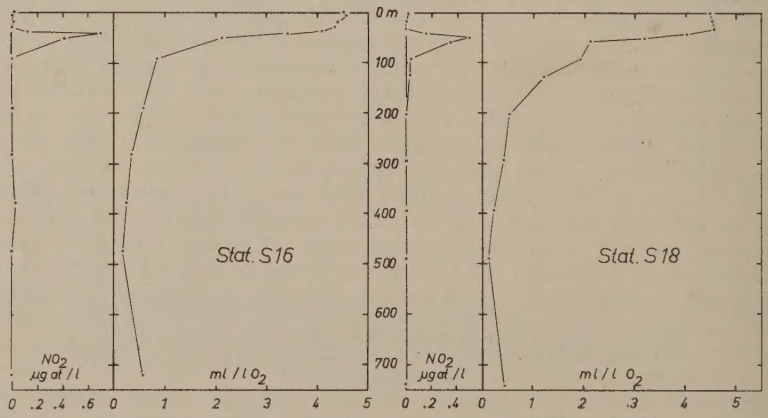

Figure 6. Vertical distribution of oxygen and nitrite south of the reduction zone. SCOPE Expedition, 1956.

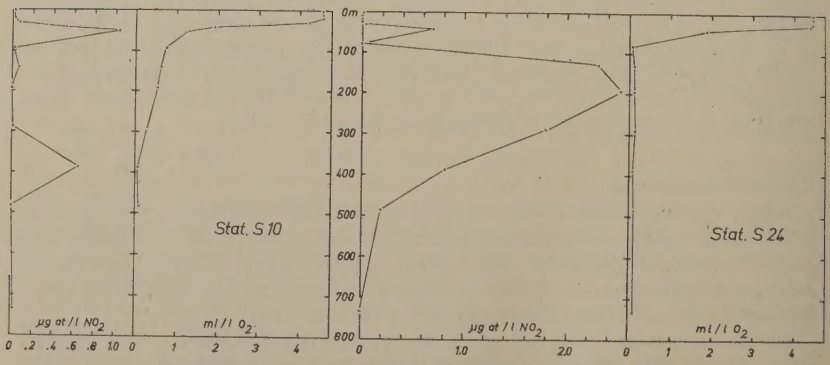

Figure 7. Vertical distribution of oxygen and nitrite in the reduction zone. SCOPE Expedition, 1956.

of the oxygen poor water, located between 150 and 1000 m depth in the north-eastern part of the Tropical Pacific. For constructing this chart only data from September to December 1955, obtained on EASTROPIC Expedition (1956), have been used. Results from other cruises into the highly productive Gulf of California reveal that oxygen poor water is also found in the Gulf. In comparing Figure 4 with Figure 1, it will be seen that only water with very low oxygen concentration below the thermocline contains nitrite in considerable amounts, which suggests reduction processes.

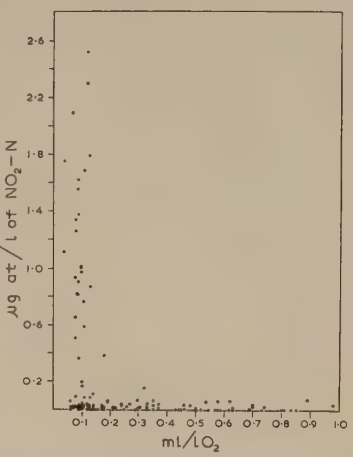

Figure 8. Nitrite versus oxygen plot. Oxygen values are not corrected for error caused by introduction of oxygen-containing Winkler reagents. SCOPE Expedition, 1956 and ISLAND CURRENT Survey, 1957.

The nitrite quantities measured are rather high. As organic matter is necessary for the bacteria to carry out the denitrification, it is assumed that the barren north-western area (BRANDHORST, 1958) is supplied with sufficient organic matter by the prevailing current (SVERDRUP *et al.*, 1942; Fig. 205). Oxygen values beyond the northern boundary of the reduction zone are still low, but only traces of nitrite can be detected (Fig. 5, Stat. S 25, IS 78). It may be possible that the bacteria do not find suitable conditions for reduction in this transition zone, being strongly influenced by the subarctic North Pacific water. The southern limit of the reduction zone apparently is caused by the higher oxygen content below the thermocline (Fig. 6, Stat. S 16, S 18).

Figure 7 illustrates the relationship between oxygen and nitrite content in the reduction zone at selected stations. At S 24 oxygen concentration rapidly decreases below the thermocline. Nitrite is being produced below 100 m and reaches the maximum value at 200 m with 2·5 μg at. N/l. The nitrite peak at station S 10 is located at a depth of about 400 m, together with the lowest oxygen value. The deep nitrite layer slopes down towards south. This cannot be explained by subsurface currents, since the corresponding surface of thermosteric anomaly does not slope.

From an oxygen versus nitrite plot, the two nitrite maxima are clearly distinguishable. Nitrite from the upper maximum is found within a wide oxygen range from about 1–5 ml/l, due to the very sharp thermocline with which this maximum is associated. Nitrite values of the deep reduction maximum occur only in water with less that 0·15 ml/l (Fig. 8). For the oxygen introduced with the Winkler reagents, one should apply a correction of 0·05 ml/l, thus this oxygen value limiting the reduction becomes 0·10 ml/l.

GILSON (1937) observed a similar deep nitrite maximum in the north-eastern part of the Arabian Sea, but did not offer an explanation at that time. By courtesy of Mr. GILSON, who supplied original, unpublished data of the "John Murray" Expedition, the author was enabled to draw a figure of the nitrite distribution in the Arabian Sea (Fig. 9). Extremely high nitrite concentrations of more than 7·5 μg at. N/l, also accompanied with low oxygen, have been measured.

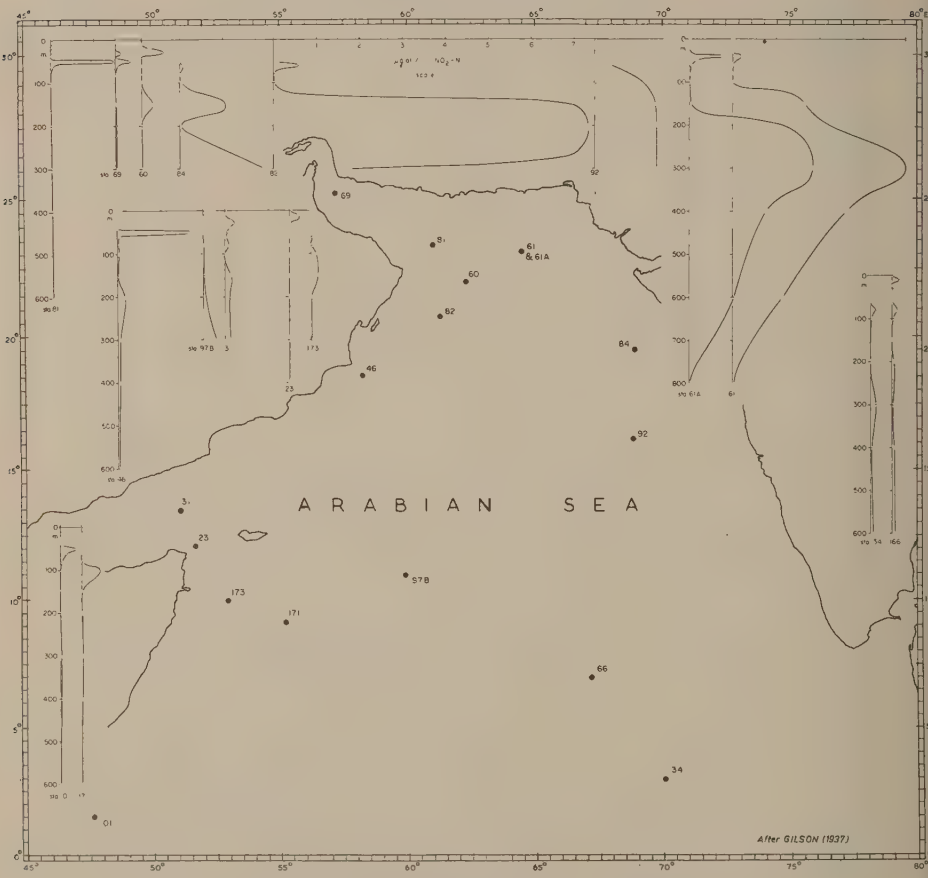

Figure 9. Occurrence of nitrite in the Arabian Sea.
Nitrite in μg at. N/l. After unpublished data of the "John Murray" Expedition by courtesy of Mr. H. C. GILSON.

The concentration of nitrite, being a very ephemeral nutrient, is determined by the balance between formation and destruction, which depends on many highly varying factors. A combined, very extensive bacteriological, chemical, and oceanographic study will be necessary to tackle the very important and interesting problem of the relationship between production and decay in their complete cycle.

Acknowledgement

For reading the manuscript and for making suggestions I am indebted to Dr. W. OHLE, Plön. This work was done partly during staff membership of the Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, La Jolla, California.

Summary

1. Over large areas of the Eastern Tropical Pacific considerable amounts of nitrite occur in the thermocline layer, due to nitrification processes associated with the remineralization of sinking planktonic material.

2. A very strong depletion of oxygen is found below the thermocline, caused by the decomposition of organic matter. This body of water with an oxygen content of less than 0·10 ml/l, observed between 100 and 1000 m depth, also contains nitrite which is being produced by reduction of nitrate. Nitrite is not apparent in water with a higher oxygen content.

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Table 1

Summary of chemical analyses

SCOPE station 2
11. Nov. 1956; 21°07·0′N, 110°03·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	28·12	34·62	4·49	0·00
15	27·65	34·63	4·30	0·00
35	27·22	34·60	4·35	tr.[1])
50	26·17	34·51	4·27	0·48
65	20·96	34·45	2·64	0·12
85	17·72	34·39	1·93	tr.[1])
118	13·36	34·11	2·08	0·00
196	12·26	34·78	–	0·00
243	11·43	34·76	–	0·00
290	10·66	34·70	0·06	0·00
388	8·89	34·58	0·25	0·00
482	7·74	34·52	0·13	–
734	5·52	34·53	0·44	0·00

SCOPE station 8
17. Nov. 1956; 11°13·0′N, 90°55·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	27·58	33·27	4·71	0·05
8	27·54	33·24	4·75	0·05
15	27·41	33·26	4·84	0·05
19	27·26	33·28	4·51	0·05
28	22·06	34·42	2·94	0·79
51	17·02	34·87	1·03	0·18
87	13·67	34·92	0·30	0·01
120	13·04	34·92	0·35	0·03
182	12·26	34·87	0·35	0·00
277	10·56	–	0·08	0·09
374	8·42	34·63	0·08	1·26
470	7·44	34·61	0·10	0·97
718	5·60	34·57	0·14	0·11

[1]) tr. = detectable traces.

SCOPE station 9A
19. Nov. 1956; 8°56·0′N, 88°29·5′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_2-N (µg at./l)
0	25·72	33·37	4·27	0·22
5	25·72	33·39	4·26	0·11
9	24·60	33·60	4·02	0·23
12	22·18	34·07	3·26	0·20
22	18·28	34·65	1·78	0·45
27	17·04	34·69	1·38	0·49
63	13·97	34·92	0·70	0·02
111	13·00	34·90	0·48	0·03
202	11·94	34·85	0·54	0·05
308	10·78	34·75	0·21	0·01
413	9·49	34·70	0·10	0·02
514	7·97	34·63	0·10	0·16
767	5·70	34·59	0·30	0·06
1035	4·47	34·61	0·83	0·00
1559	3·08	34·61	–	0·00

SCOPE station 10
24. Nov. 1956; 8°42·0′N, 86°01·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_2-N (µg at./l)
0	26·86	32·65	4·56	0·02
20	26·79	32·68	4·55	0·02
30	25·94	33·11	4·20	0·06
37	23·00	33·93	2·74	0·32
42	19·54	34·49	1·91	0·52
51	16·92	34·74	1·30	1·04
96	13·14	34·87	0·74	0·02
142	12·54	34·83	0·62	0·06
196	11·94	34·83	0·55	0·00
290	10·72	34·74	0·30	0·01
388	9·06	34·67	0·08	0·65
484	7·85	34·65	0.10	0·00
736	5·78	34·60	–	0·02

SCOPE station 11
25. Nov. 1956; 7°37·0′N, 82°25·5′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_2-N (µg at./l)
0	26·72	29·40	–	0·00
15	26·76	29·70	–	0·00
30	25·82	31·82	–	0·00
44	23·04	33·48	–	1·45
53	18·70	34·51	–	0·19
59	17·03	34·78	–	0·05
91	15·22	34·88	–	tr.
127	14·14	34·93	–	tr.
205	12·68	34·89	–	0·00
300	11·12	34·82	–	0·00
406	9·32	34·69	–	0·00
507	7·97	34·65	–	0·00
769	5·83	34·59	–	0·00

SCOPE station 16
1. Dec. 1956; 5°59·0′N, 79°48·8′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	26·68	28·30	4·52	0·02
6	26·50	28·38	4·57	0·00
18	26·62	30·61	4·40	0·01
29	25·94	33·11	4·35	0·00
39	24·32	33·61	4·10	0·13
43	23·03	33·93	3·42	0·69
52	19·43	34·66	2·13	0·41
94	14·34	34·96	0·85	0·00
190	13·16	34·97	0·59	0·00
283	11·94	34·88	0·33	0·00
379	9·37	34·72	0·24	0·03
472	8·42	34·69	0·17	0·00
720	6·09	34·60	0·57	0·00

SCOPE station 17
2. Dec. 1956; 4°09·0′N, 83°34·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	27·02	32·96	4·43	0·02
9	26·42	32·95	4·50	0·02
18	26·38	33·01	4·48	0·03
27	25·54	33·36	4·18	0·11
30	24·45	33·64	3·94	0·24
37	20·64	34·31	2·78	0·54
49	18·50	34·70	2·15	0·67
97	14·76	34·97	1·46	0·03
197	13·22	34·96	0·63	0·00
292	11·74	34·88	0.33	tr.
394	9·34	34·70	0·14	tr.
490	8·05	34·67	0·22	0·01
743	5·86	34·61	0·69	tr.

SCOPE station 18
3. Dec. 1956; 5°28·5′N, 86°57·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	26·42	33·17	4·45	0·01
15	26·10	33·15	4·51	0·00
30	25·95	33·28	4·56	0·00
41	24·05	33·73	4·03	0·16
47	21·70	34·36	3·19	0·49
56	18·05	34·94	2·13	0·35
91	16·76	35·03	1·93	0·04
124	14·96	34·96	1·18	0·03
199	13·16	34·97	0·52	0·00
292	12·41	34·90	0·43	0·00
391	11·06	34·79	0·21	0·00
485	8·97	34·70	0·12	0·00
736	6·07	34·59	0·44	0·00

SCOPE station 19
4. Dec. 1956; 6°46·0′N, 89°52·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	27·06	32·51	4·39	0·01
7	26·74	32·51	4·37	0·00
18	26·50	32·95	4·33	0·03
24	23·92	33·88	3·06	0·16
29	21·06	34·53	2·53	0·40
35	17·83	34·66	1·16	1·07
47	15·46	34·88	1·40	0·73

94	13·57	34·97	0·98	0·04
190	12·66	34·88	0·73	0·00
283	11·52	34·85	0·58	0·00
380	10·24	34·74	0·62	0·00
474	9·02	34·69	0·17	0·01
722	6·03	34·60	0·13	0·00

SCOPE station 20B
6. Dec. 1956; 7°52·0′N, 91°19·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (μg at./l)
0	25·60	33·24	4·20	0·07
6	25·62	33·24	4·22	0·07
15	23·35	33·65	3·36	0·10
18	19·31	34·51	1·68	0·19
21	17·66	34·67	1·41	0·21
49	13·99	34·78	0·58	0·06
98	12·70	34·88	0·37	0·01
194	11·31	34·83	0·80	0·00
285	10·58	34·78	0·80	0·00
379	9·56	34·71	0·26	0·02
468	8·39	34·70	0·17	0·00
705	6·32	34·61	0·46	0·00
951	5·03	34·60	0·46	–
1411	3·42	34·64	1·25	–
1915	2·46	34·69	1·98	–

SCOPE station 21
7. Dec. 1956; 12°17·0′N, 96°50·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (μg at./l)
0	25·44	33·61	4·56	0·08
8	25·40	33·61	4·55	0·07
31	23·82	33·93	4·48	0·18
38	21·70	34·23	4·24	0·62
52	19·98	34·43	3·92	0·47
67	18·03	34·54	2·59	0·83
75	16·89	34·65	1·86	0·77
129	12·64	34·89	0·29	0·00
205	11·60	34·81	0·11	0·08
300	10·22	34·74	0·13	0·08
402	8·64	34·65	–	1·21
498	7·18	34·61	0·11	0·58
736	5·44	34·56	0·10	0·00

SCOPE station 22
8. Dec. 1956; 14°37·0′N, 100°09·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (μg at./l)
0	29·48	33·97	4·56	0·12
4	25·17	34·00	4·47	0·15
8	24·78	34·02	4·53	0·16
16	23·96	34·09	4·47	0·22
26	22·48	34·18	4·11	0·39
39	20·95	34·28	4·05	0·48
49	20·10	34·45	1·53	0·22
76	16·21	34·72	0·32	0·15
144	12·85	34·87	0·14	0·00
214	12·00	34·83	0·09	0·00
293	11·10	34·76	0·09	1·63
373	10·00	34·70	0·09	0·81
596	6·96	34·57	0·09	0·36

SCOPE station 23
9. Dec. 1956; 16°52·0′N, 103°06·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	29·04	34·05	4·42	0·01
10	28·29	34·06	4·34	0·00
30	28·46	34·24	4·45	0·00
35	28·46	34·33	4·40	0·00
52	24·07	34·34	3·90	0·49
63	20·97	34·54	1·98	0·23
75	18·64	34·54	0·89	0·07
120	13·64	34·85	0·13	0·87
197	12·06	34·83	0·09	1·55
291	10·98	34·76	0·09	1·38
390	9·68	34·69	0·10	1·00
485	8·28	34·61	0·11	0·76
737	6·05	34·56	0·10	0·02

SCOPE station 24
10. Dec. 1956; 19°30·0′N, 105°52·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	26·92	34·65	4·45	0·01
6	26·94	34·86	4·46	0·00
18	26·88	34·65	4·44	0·00
24	26·46	34·77	4·36	0·00
30	22·38	34·36	4·34	0·04
43	18·99	34·42	1·88	0·69
80	14·84	34·74	0·09	0·00
131	12·80	34·84	0·12	2·30
196	11·80	34·80	0·12	2·52
290	10·63	34·74	0·13	1·79
388	9·41	34·67	0·09	0·81
484	8·08	34·60	0·10	0·19
733	5·91	34·58	0·09	0·00

SCOPE station 25
12. Dec. 1956; 23°31·0′N, 111°22·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	23·82	34·70	4·46	0·00
5	23·76	34·70	4·70	0·01
15	23·73	34·66	4·67	0·00
30	23·54	34·68	4·66	0·00
45	23·49	34·70	4·53	0·01
53	22·38	34·59	4·41	0·25
82	15·34	33·95	3·88	0·07
142	13·23	34·61	0·39	0·02
196	11·92	34·71	0·15	0·00
242	11·38	34·72	0·10	0·01
289	10·56	34·69	0·15	0·02
390	8·88	34·59	0·13	0·00
486	7·80	34·54	0·12	0·02

ISLAND SURVEY station 4
13. May 1957; 19°31·5′N, 114°56·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_3-N (µg at./l)
0	23·99	34·19	5·54	0·01
43	23·00	34·33	5·70	0·00
64	21·84	34·35	5·74	0·01
78	19·39	34·19	5·01	0·25
92	16·68	34·25	3·50	0·48
116	13·40	34·11	2·15	0·04
170	12·36	34·65	0·33	0·02

273	10·87	34·71	0·18	0·38
320	10·26	34·67	0·09	1·62
378	8·96	34·60	0·15	0·02
453	8·08	34·59	0·12	0·03
548	7·10	34·54	0·10	0·01
654	6·20	34·52	0·15	tr.
814	5·12	34·54	0·30	tr.
974	4·49	34·60	0·50	tr.
1179	3·84	34·60	0·63	0·01

ISLAND SURVEY station 29
23. May, 1957; 18°17·6′N, 114°48·1′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_2-N (μg at./l)
0	24·80	34·08	3·78	0·03
14	24·72	34·11	3·76	0·01
33	23·13	34·38	3·96	0·00
58	19·20	34·15	3·43	0·33
73	16·63	34·25	1·66	0·23
83	14·52	34·02	2·15	0·16
117	12·39	34·38	0·70	0·03
174	11·86	34·83	0·09	0·03
245	10·92	34·70	0·09	0·90
293	10·21	34·68	0·11	1·69
347	9·65	34·70	0·08	1·34
421	8·62	34·61	0·07	0·02
494	7·64	34·56	0·09	0·01
597	6·84	34·53	0·08	0·02
749	5·66	34·54	0·18	0·01
894	4·88	34·53	0·17	0·02

ISLAND SURVEY station 51
2. June, 1957; 16°50·1′N, 117°30·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_2-N (μg at./l)
0	24·82	34·24	4·12	0·00
20	24·84	34·16	4·09	0·00
40	24·05	34·11	4·17	0·05
60	23·06	34·23	4·12	0·10
86	19·58	34·34	1·99	1·04
101	16·51	34·25	1·68	0·24
127	13·91	34·52	0·27	0·04
157	12·97	34·67	0·06	0·06
208	11·70	34·71	0·08	0·93
258	11·03	34·71	0·04	1·11
312	10·39	34·69	0·04	1·75
414	8·98	34·54	0·08	0·50
565	7·10	34·50	0·10	0·04
721	5·95	34·49	0·15	0·00
926	4·94	34·48	0·19	0·05
1127	4·16	34·52	0·37	0·04

ISLAND SURVEY station 77
9. June, 1957; 20°46·0′N, 111°59·0′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_2-N (μg at./l)
0	22·52	34·71	4·28	0·00
54	21·22	34·56	4·37	0·02
73	19·38	34·39	4·26	0·10
98	16·14	34·49	1·78	0·09
119	14·24	34·60	0·46	0·03
144	13·48	34·69	0·24	0·02
164	12·90	34·74	0·14	0·01
230	11·75	34·76	0·07	2·09

322	9·92	34·60	0·09	0·01
437	8·51	34·60	0·07	0·01
550	6·98	34·44	0·10	0·02
660	6·18	34·51	0·10	0·02

ISLAND SURVEY station 78
10. June, 1957; 22°32·2′N, 112°52·5′W

Depth (m)	Temp. (°C)	S ‰	O_2 (ml/l)	NO_2-N (μg at./l)
0	20·22	34·38	4·69	0·01
58	18·02	34·37	4·47	0·37
76	16·64	34·33	3·86	0·40
126	13·29	34·67	0·33	0·04
192	11·58	34·70	0·12	0·02
236	10·98	34·69	0·08	0·01
286	10·28	34·68	0·09	0·01
470	7·73	34·52	0·06	0·02

Benthos Densities off Tropical West Africa

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Introduction

In the absence of reef-building organisms the benthos of the continental shelf of tropical West Africa bears a close resemblance to that of the Mediterranean and Western Europe and faunistic communities may be recognized which parallel those familiar to the European marine ecologist and which, because of the zoogeographical relationships between the areas, include many identical organisms. Comparison, therefore, of quantitative data on the abundance and size of individuals from the West African region with what is already known of temperate and arctic seas is desirable; the recent faunistic survey with quantitative samplers off West Africa (LONGHURST, 1958) has provided, incidentally, some information on *faunal indices* (biomass per unit area, species per sample or station, individuals per unit area) which is analysed and presented here.

The survey covered the continental shelf between the Gambia River (13°10′N) and the Sulima River (06°05′N) at the Sierra Leone — Liberian border; for convenience of reference, three sectors of the shelf in this region were recognized — the St. Ann shelf, the Guinea shelf, and the Senegal shelf — and these have been described hydrographically and topographically in the faunistic survey. A total of 158 stations was worked in these three sectors, mostly arranged in transects running out from the coast to the continental edge.

The nature of the sampling and the validity of the standard station procedure was tested statistically with several series of replicate hauls; these results have been analysed in a recent review of the sampling problem in benthic ecology (LONGHURST, 1959) and from this analysis it was quite clear that quantitative data with conventional grabs in this area must be based minimally on a 5 haul, 0·5 m^2, sample and that data from the single haul surveys of BUCHANAN (1958) and SPÄRCK (1951) off the West African coast may be used only with reservations in comparative work.

The interest of the faunal indices lies in the correlations which may be expected between their value and that of the basic productivity of the hydrographic regime of the overlying water mass and, for comparative purposes, the digestion of the data to a minimum number of comprehensive figures representative of the area is in theory desirable but in practice unsatisfactory.

Table 1

Bathymetric variation of the faunal indices on each shelf sector. (A – values for shallow shelf communities, B – values for deep shelf communities as defined in Longhurst, 1958)

		St. Ann			Guinea			Senegal		
		Spp./ sample	Ind./m²	g/m²	Spp./ sample	Ind./m²	g/m²	Spp./ sample	Ind./m²	g/m²
	Estuarine	–	–	–	4·06	122·0	137·1	–	–	–
A	0– 20 m	13·17	84·52	11·22	17·32	110·3	15·15	19·00	822·0	74·23
	20– 40 m	15·14	83·85	15·16	22·79	140·0	11·96	24·70	1386·0	27·50
	40– 60 m	24·45	86·85	15·15	17·25	43·50	8·50	21·00	117·0	11·28
	over 60 m	22·00	74·00	16·48	5·00	20·00	4·76	–	–	–
B	50–100 m	19·00	72·00	12·76	5·50	16·00	0·85	21·01	76·33	16·15
	100–150 m	23·60	41·50	3·02	7·00	45·10	3·02	–	–	–
	150–160 m	5·50	31·00	1·51	8·00	72·00	7·04	8·50	54·50	34·62
	200–250 m	8·00	22·00	2·90	3·00	15·00	3·50	–	–	–
	250–350 m	–	–	–	2·00	23·00	3·03	–	–	–

SPÄRCK (1935) used such figures in a way which is certainly an oversimplification and it seems most satisfactory to use indices which are representative of parallel ecological situations within each of the areas to be compared.

However, the division of a survey area into ecological units for this purpose presents certain difficulties; such a division may be based upon the biological communities, upon differences in the hydrographic regime, or upon differences in the deposits. There is no prior indication as to which of these factors would be the most satisfactory and analysis of the present data is made in terms of all three possibilities.

Variation with the Nature of the Water Mass

The hydrographic stability and the presence of a permanent discontinuity layer in this region (WATTS, 1958; LONGHURST, 1958) enables a single factor, depth, to be used to indicate hydrographic conditions. From Table 1 it may be seen that there is a general decline in the values of the faunal indices with increasing depth in each shelf sector, and it should be noted that the number of stations is apparently insufficient to demonstrate the occurrence, or otherwise, of a discontinuity in these values at the level of the thermocline, though such discontinuities have been demonstrated for communities of benthic invertebrates and demersal fish (POSTEL, 1955; SALZEN, 1957; LONGHURST, 1958).

The trend of the relationship is not regular, yet the anomalies are generally explicable on reference to the original station sheets, being due either to the occurrence of single species concentrations, to isolated very large or heavy organisms, or to an overall richness or poverty of the fauna. Two important bathymetric changes in the fauna may be related to the decline in the faunal indices — a change in the relative importance of the various groups of animals in the fauna, and a general reduction in its diversity, both trends being independent of the discontinuity of community type associated with the thermocline or

the δt discontinuity. In accordance with expectation (e. g., THORSON, 1951) molluscs are of decreasing importance towards the continental edge while echinoderms become increasingly prominent.

There is considerable similarity between the values from the neighbouring St. Ann and Guinea shelf sectors while the values for biomass and individuals are considerably higher from the Senegal sector — in detail, due to higher numbers of small crustacea, especially tanaids and amphipods, and to a small number of unusually large lamellibranchs (*Cardium*, *Mactra*) inshore. This disparity between the Senegal and the other sectors may be explicable in terms of the different hydrographic influences in the two regions — the St. Ann/Guinea area is under the influence of the relatively warm and unproductive Guinea Current with only a small annual influent from the colder, richer Canary Current (WATTS, 1958), whilst the Senegal shelf is wholly under the influence of the Canary Current.

The values of the faunal indices from estuarine stations reflect two characteristics of the estuarine fauna in this region — a general and progressive decline in diversity with increasing distance from the sea, and the occurrence of relatively great single species concentrations, in particular of the gastropod *Pachymelania aurita* ($>1700/m^2$) and the polychaete *Pectinaria sourei* ($>680/m^2$); comparable figures were recorded offshore at only one station (MB2/A8 on the Guinea shelf) where a concentration of *Pecten jacobeus* was encountered.

Variation with the Nature of the Deposits

The techniques used in the analysis of the deposits have already been described (LONGHURST, 1958) and permit description of the soil from four aspects — the percentage of silt, or soft organic material; the weighted mean particle size; the sorting coefficient; and gradation by eye and microscopically. It might be expected that there would be a simple relationship between the first two variables — the percentage of silt and the grade of the deposits — and that these could be considered together in relation to the fauna; this would be true only if the macro-particles were composed solely of transported matter, but in fact the simple relationship is obscured by the inclusion in the particle size distribution of large particles of local organic origin. A very soft mud containing large particles of locally produced shell is a very common type of deposit yet has an apparently anomalous silt/grade relationship.

However, the distribution of the fauna is probably most influenced by the percentage of silt deposited — the softness of the deposits — and analysis of the faunistic data is made in relation to this factor.

The correlation between density of the fauna and depth necessitates separation of the effects of depth and silt content. In Table 2 the data from all non-estuarine stations on the St. Ann and Guinea shelves is analysed in this respect.

This table shows, in the first two columns, that there is no overall relationship between depth and silt content regardless of the restriction of the very soft deposits to relatively shallow water — in fact, no deposits with a silt content greater than 70% occurred deeper than 70–80 m. It is also clear from the table that even if it is legitimate on this account to ignore the depth factor there is still no correlation over so large an area between the silt content and faunal indices and in an attempt to establish such a correlation the analysis was restricted to shallow water and to progressively smaller geographical areas.

Table 2

Variation of the faunal indices with silt content of the deposits; silt content determined by a sedimentation method. All non-estuarine stations which were occupied on the St. Ann/Guinea shelf sectors

Silt (%)	Mean depth (m)	Number of samples	Spp./sample	Ind./m²	g/m²
0– 10	48	12	12·08	39·91	6·73
10– 20	66	21	13·33	163·47	12·73
20– 30	20	16	23·50	268·25	10·11
30– 40	51	13	17·76	115·84	8·25
40– 50	55	19	20·47	84·52	13·75
50– 60	35	7	18·85	236·85	11.53
60– 70	75	10	13·20	70·20	7·69
70– 80	26	6	19·50	98·83	20·98
80–100	21	12	13·66	78·25	15·98

Thus, Table 3 includes data from all stations worked on the Guinea shelf sector in less than 40 m of water with the omission of a few isolated stations off the Isles de Los, Guinea. In this considerably more restricted area there becomes apparent in the data a tendency for the higher values of the faunal indices to be restricted to the middle of the range of silt content values — a rich fauna does not develop either on very clean sand or on very soft mud. Within an even more restricted area the same thing is again evident; completely independent data from 28 inshore stations between Cape Sierra Leone and the Banana Islands shows a tendency for the high values to be concentrated in the centre of the field, low values at the extremes.

Sub-samples of the soil taken at each station included for analysis in Table 3 were graded in a series from coarse to fine deposits by eye and microscopically, and it was hoped that this might provide independent evidence of any correlation between grade of deposits and density of the fauna. But it became clear that there is no correlation either with the objective measurement of the soil grade or with the values of the faunal indices and that this method of grading is apparently quite unsound.

The degree of sorting (S)[1] of the deposits will have an influence on the density of the fauna and this is analysed in Table 4 for the data already mentioned from 28 inshore stations off Sierra Leone. No correlation was immediately obvious and the relationship between (S) and the faunal indices was investigated statistically, with the following result:—

	g/m²	Individuals/m²	Species/sample
r	0·42	0·58	0·21
t	2·49	5·39	1·26
P	0·02	0·001	0·20

This analysis indicates a positive correlation between S and the faunal

[1] The sorting coefficient S is an indication of the uniformity of grade of the soil particles and is derived from $S = Q_1/Q_3$ where Q_1 and Q_3 are the first and third quartile diameters of the particle size distribution. In a well-sorted deposit these approach the median diameter, and S tends towards unity.

Table 3

Variation of the faunal indices with silt content of the deposits; all stations which were occupied on the Guinea shelf between Yelibuya Sound and the Banana Islands, all shallower than 40 m

Silt (%)	Spp./sample	Ind./m²	g/m²
0– 10	18·00	70·80	8·61
10– 20	19·22	154·60	21·70
20– 30	25·50	365·70	10·23
30– 40	20·50	129·60	9·68
40– 50	24·50	117·70	12·48
50– 60	25·15	274·10	13·18
60– 70	15·57	90·15	15·68
70–100	11·60	79·60	7·60

Table 4

Variation of faunal indices with increasing values of sorting coefficient (S); data from 28 stations occupied inshore between Cape Sierra Leone and the Banana Islands, gear van Veen grab from open launches

(S)	g/m²	Ind./m²	Spp./sample	(S)	g/m²	Ind./m²	Spp./sample
1·40	1·56	14	5	2·25	1·66	26	12
1·50	10·66	72	19	2·25	14·26	88	18
1·50	2·89	46	10	2·33	10·58	70	25
1·50	2·30	18	7	3·00	4·54	40	13
1·50	2·35	104	14	3·00	7·42	28	10
1·64	1·26	44	12	3·40	5·46	30	16
1·71	19·46	148	25	3·80	2·68	2	5
1·76	7·60	106	25	4·00	24·60	202	34
1·83	5·38	36	15	5·40	7·71	92	15
1·87	16·83	90	23	5·90	4·00	48	10
2·01	24·24	78	25	6·20	1650·00	134	32
2·04	13·30	40	16	10·00	14·42	140	29
2·06	9·80	16	5	14·00	11·82	90	23
2·23	18·18	74	23	20·00	24·70	186	21

indices which is strongest (and most significant) in the case of individuals and weakest (and least significant) in the case of species. Thus as the sorting coefficient becomes higher and the deposits less well sorted (that is, having a large range in the particle size distribution) so the fauna tends to become more dense; that this is not due simply to the presumed increased possibilities of ecological diversity in such deposits is shown by the lack of parallel increase in the number of species per unit area.

Table 5

Variation of the faunal indices with the nature of the biological communities; the category deep includes both the deep shelf community and the continental slope community as defined in Longhurst, 1958

	St. Ann			Guinea			Senegal		
	Spp./ sample	Ind./m²	g/m²	Spp./ sample	Ind./m²	g/m²	Spp./ sample	Ind./m²	g/m²
Offshore:									
Venus	7·20	77·00	11·96	16·04	94·62	7·84	18·90	1141·6	47·80
Transitional	23·20	79·20	15·80	22·70	240·80	15·50	17·50	431·0	98·70
Amphioplus	14·20	89·10	12·80	14·40	76·80	13·70	16·50	115·0	19·3
Deep	14·00	41·60	5·77	6·40	42·80	4·36	7·62	32·7	13·5
Estuarine:									
Amphioplus				13·00	290·20	6·11			
Pachmelania				5·00	358·0	494·4			
Others				4·30	73·30	2·74			

Variation with Community Type

The variation of the faunal indices with the nature of the faunal communities is analysed for each sector of the continental shelf in Table 5; the communities recognized in this analysis are those described in the faunistic survey with the omission of most hard substrate communities — it is virtually impossible to obtain a satisfactory quantitative collection from most rocky or stony bottoms.

There are considerable similarities between the presentation of the data in Table 5 and the analysis by depth of Table 1. In each case the values for individuals and for biomass are higher on the Senegal sector in shallow water than on the other two sectors, while the number of species is rather similar in all three.

Except on the Senegal shelf the values for the *Venus* and the *Amphioplus* communities, despite differences in the constituent species, show a considerable degree of similarity while the transitional faunas include higher values for both species and individuals; this appears to contradict the previous finding that the *Venus* community includes the greater number of species, and the two facts taken together appear to carry an implication of greater diversity between stations in this community.

Discussion

In the foregoing analysis of the quantitative data it is clear that, with limitations, some degree of correlation can be obtained between the faunal indices and those biological and environmental factors which can be used as the second variable in the analysis. It is also clear that in a survey of this nature, which attempts to cover a wide geographical area — probably, as the results show, too wide for the resources and time available — an analysis in terms of depth or deposits presents considerable difficulty. In the first case, the slope of the continental shelf and the nature of the continental edge make it very difficult to work transect lines which sample adequately throughout

their length and bathymetric range; in the second case, unless the stations are sufficiently close to each other and are restricted to a small geographical area, the correlation between deposit and fauna is obscured by the patchiness of the latter, due to larval fall-out and other biological factors. A deposit optimum may be readily determined for a particular species, as WEBB (1956) has done for *Amphioxus* in Lagos lagoon, but clearly over a large part of its range a species will not necessarily occur in the same, or even nearly the same density, wherever the optimum conditions occur.

Disagreement on the methods of classification of benthic communities does not prevent general agreement that they are the product of, and are indicative of, the deposit and hydrographical complex in which they occur. For this reason, the results of the quantitative survey are probably best expressed for comparative purposes in terms of the faunistic communities in the relevant areas. Table 5, then, should provide the definitive data from the survey.

It is not appropriate here to attempt comparison between these results and those of similar surveys scattered throughout the literature nor is it easy to make comparison even with the other West African data. BUCHANAN (1958), like STEPHEN (1933), was working in an area in which the uncontorted nature of the coastline produced a strict seaward sequence of zones of deposit types, and it is on these zones, following the recommendations of JONES (1950), that he based his community classification. However, the classification used in the present paper is based — in the shallower regions at least — on the composition of the fauna, for it was found in the faunistic survey to be difficult to agree with JONES' proposed *sand*, *muddy-sand*, *mud* division of the shelf fauna; in a survey of wide geographical scope it is quite impossible to recognize the reality of such arbitrary divisions between two variable components of the deposits — especially when a third, the calcareous component, is found to be important.

BUCHANAN's data, unfortunately includes only biomass figures which are, for a number of reasons, the least satisfactory of the faunal indices; his figures — *fine sand* (120 g/m^2), *sandy-silt* (540 g/m^2), *silty-sand* (38 g/m^2), *coarse sand* (28 g/m^2) — are, at first sight, considerably in excess of the figures from the present survey. However, his very high figures are due without exception to single species concentrations: *Owenia fusiformis* in the case of fine sand, and *Turitella annulata* in the case of sandy silt. Without these species the figures become 8 g/m^2 and 40 g/m^2 respectively. The values for the other deposits include a high proportion of forms having heavy calcareous exoskeletons, such as the foraminiferan *Julienella* which was not important in the fauna covered by the Guinea survey. Accra, the site of BUCHANAN's survey, is an area of hydrographic instability caused debatably by local coastal upwelling (WATTS, 1958) or by seasonal influx of cold water of Benguelan origin (BUCHANAN, 1958) and it might be expected to have a higher density of benthic fauna than the St. Ann or Guinea sectors where the tropical surface water lies above a stable thermocline throughout the year, and this appears to be so. Means for communities comparable with those of BUCHANAN's fine sand community and sandy-silt community have been recorded only in the Guinea sector estuaries where a dense phytoplankton bloom occurs during the dry season (BAINBRIDGE, 1959), and on the Senegal sector under the influence of the productive Canary Current.

SPÄRCK (1951) has divided data from the continental shelf of West Africa in the Volta and Congo regions into two depth zones. In the shallow water of less than 10 m his biomass means are between 30–40 g/m^2, while between

10–100 m the corresponding figures vary from 1–10 g/m². These figures lie within the range of variation found for the Guinea coast, and with allowance for different techniques of sampling and expression of data the results show no evidence of a fauna substantially richer or poorer. SPÄRCK's figures at similar depth ranges off Angola and the Walvis Bay region give evidence (40–100 g/m², 150–300 g/m² respectively) of progressive richness of the fauna as the influence of the Benguela Current becomes more evident, and here, if a comparison of absolute values is valid, the figures are somewhat higher than the means for the Senegal shelf under the less well developed counterpart of the Benguela Current of the northern hemisphere.

This survey may illustrate, perhaps, the desirability of quantitative work in this field on a comparative basis and clearly outlines two pre-requisites for satisfaction in such analysis — an adequate *ecological* coverage in each area investigated, and *standardization* of techniques and expression between individual investigators.

Summary

The quantitative data from a faunistic survey of benthos on the continental shelf of tropical West Africa shows that a relationship may be demonstrated between the density of the fauna (in terms of biomass and numbers of species and individuals per unit area) and biological and physical factors in the environment. With limitations, the fauna is most dense in shallow water, on deposits of moderate silt content, and to a certain extent in faunas transitional between *Venus* and *Amphioplus* communities. The fauna is more dense off the Gambia River than off Sierra Leone, and is more dense in the Sierra Leone estuaries than on the adjacent open shelf.

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The Multiplane Kite-Otter as a Depressor for High-Speed Plankton Samplers

By

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Introduction

For some years we have been concerned with the problem of sampling larval and juvenile fish. This problem is complicated by the marked vertical and horizontal patchiness of postlarval and juvenile fish and their ability to avoid slow moving nets during daylight hours. The use of simultaneous high-speed, horizontal hauls with a number of nets on a single towing warp appears to be the most adequate method of sampling. To accomplish this, a depressor is needed that will allow us to sample down to at least 150 m at speeds up to 10 knots.

Barnes (1951) has described the use of the multiplane kite-otter for depth control of horizontal hauls. This gear is used extensively in mine sweeping work both as a diverter and as a depressor. Barnes' tows were made at slow speeds (4·5 knots), using relatively large diameter towing wire and a heavy depressor. At his suggestion (personal communication), we ran a series of depth calibration trials at speeds of 5, 7, and 10 knots using $\frac{1}{4}$ inch and $\frac{1}{2}$ inch towing wire with a 60 pound depressor. These data are presented here as the stability and diving characteristics of the multiplane kite-otter suggest its usefulness in many phases of oceanographic research.

Description of Multiplane Kite-Otter

There are three sizes of multiplane kite-otters used in mine sweeping operations, the dimensions, weight, and tow loads of which are given in Figure 1. The gear consists of a rectangular frame with four transverse curved plates set at an angle, the side plates of the frame being inclined to give lateral stability.

A detailed drawing of the 60 pound multiplane kite-otter used in the calibration trials is shown in Figure 2. When used as a depressor, the multiplane

U.S. NAVY NUMBER		#1	#4	#5
WEIGHT–LBS.		500	180	60
APPROXIMATE TOW LOAD	5K	3800 LBS	2600 LBS.	800 LBS
	7K			1800 LBS.
	10K	14,000 LBS.	6000 LBS.	3000 LBS
DIMENSIONS	A	5'-5-3/4"	3'-10-1/2"	3'-0-3/4"
	B	5'-2-1/2"	3'–8"	2'-10-1/4"
	C	9"	6-7/8"	5"
	D	4'-3-1/2"	3'–0 1/4"	2'–4"

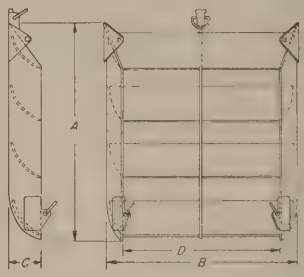

Figure 1. Dimensional sketch and specifications of U.S. Navy Type "O" multiplane kite-otter.

kite-otter is rigged with a three-point chain bridle. The lengths of the chain bridle legs are critical and must be correctly adjusted to keep the depressor towing directly astern of its tow point. The depressor will veer towards the shorter leg. Minor adjustments are made with a turnbuckle on one of the forward legs.

Methods

Two calibrations were necessary; one to determine the depressor depth at specified towing speeds with various wire sizes and wire scopes, and another to determine the wire profile with the depressor at specific depths. Two towing wire sizes were used; $\frac{1}{4}$ inch diameter, 7×19 galvanized preformed wire and $\frac{1}{2}$ inch diameter, 6×19 galvanized preformed wire. Wire vibration at speeds greater than 7 knots was considerable. Coil spring shock absorbers placed between the warp and the multiplane and at the end of the towing boom reduced this vibration considerably.

Depressor depth calibration

The depth calibration was accomplished as follows. With the ship stopped, a wire stop was secured just above the bridle and the depressor lowered to 10 m. After the ship had attained the desired towing speed, a bathythermograph was slid down the towing wire and the depressor retrieved at towing speed. The procedure was repeated at 10 m intervals until the length of wire out was more than twice the depressor depth. This was considered to be the maximum practical depressor depth as the amount of wire needed to obtain greater depths would be excessive. Depth calibration curves for $\frac{1}{4}$ inch wire at speeds of 5, 7, and 10 knots and for the $\frac{1}{2}$ inch wire at speeds of 7 and 10 knots are given in Figure 3.

Wire profile calibration

The wire profile for various depressor depths was determined from bathythermograph readings with the wire stop secured at successive 10 m intervals from the terminal end to the surface. For $\frac{1}{4}$ inch wire the depressor depths used were 50, 75, and 150 m at towing speeds of 5 and 7 knots and 50, 75, and 100 m

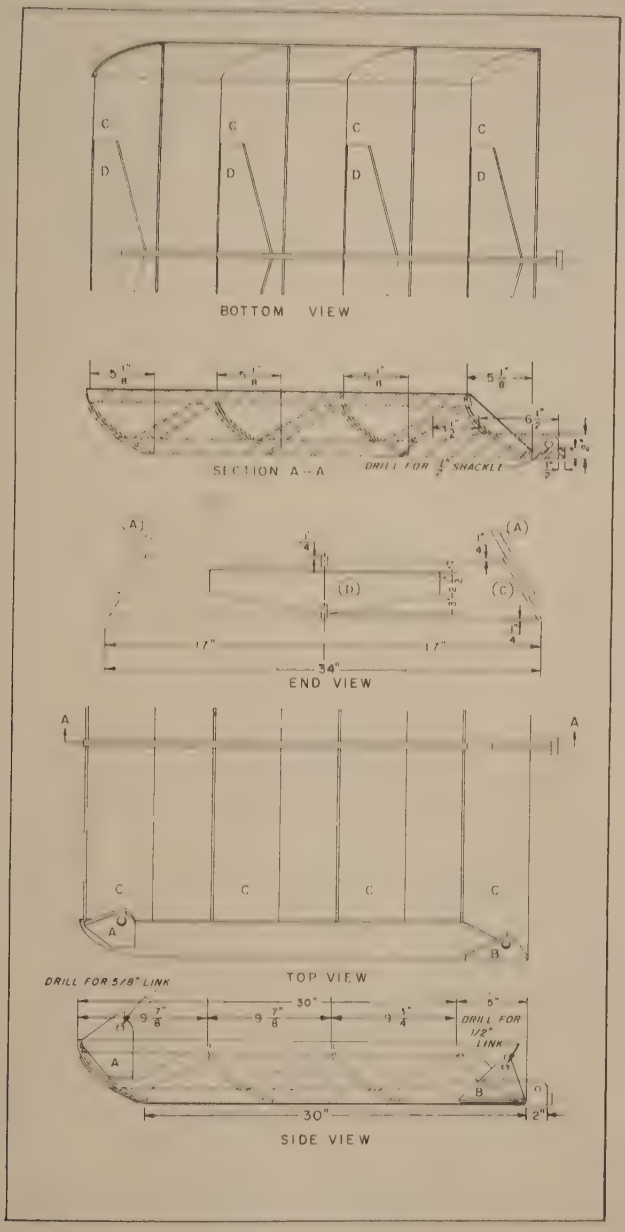

Figure 2A. Detail drawing of 60 pound multiplane kite-otter.

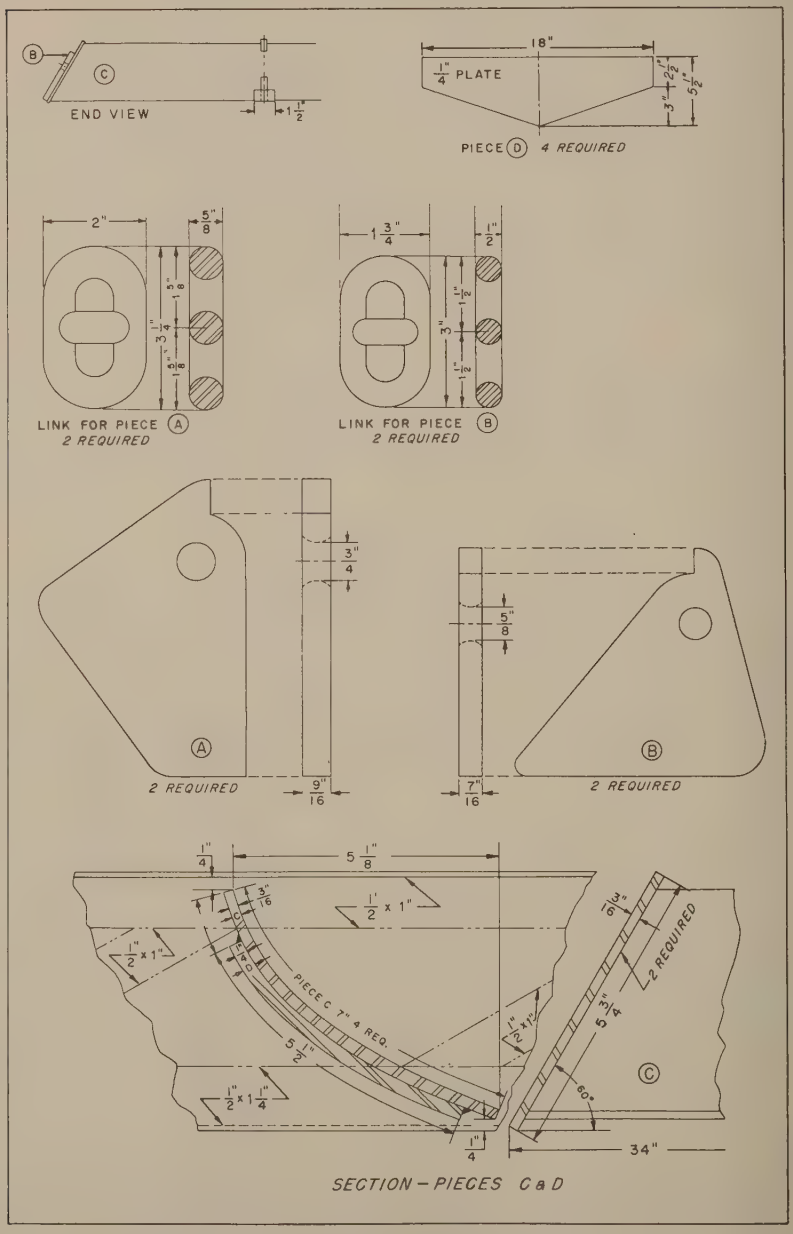

Figure 2B. Detail drawing of 60 pound multiplane kite-otter.

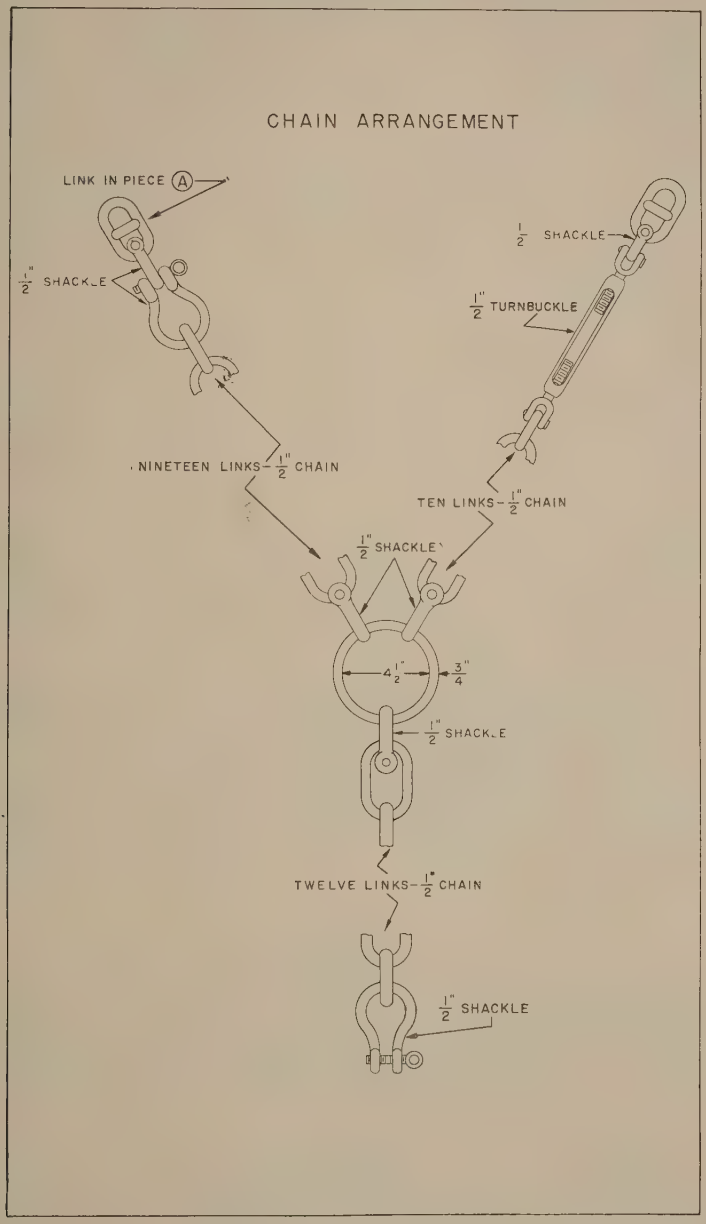

Figure 2C. Detail drawing of 60 pound multiplane kite-otter.

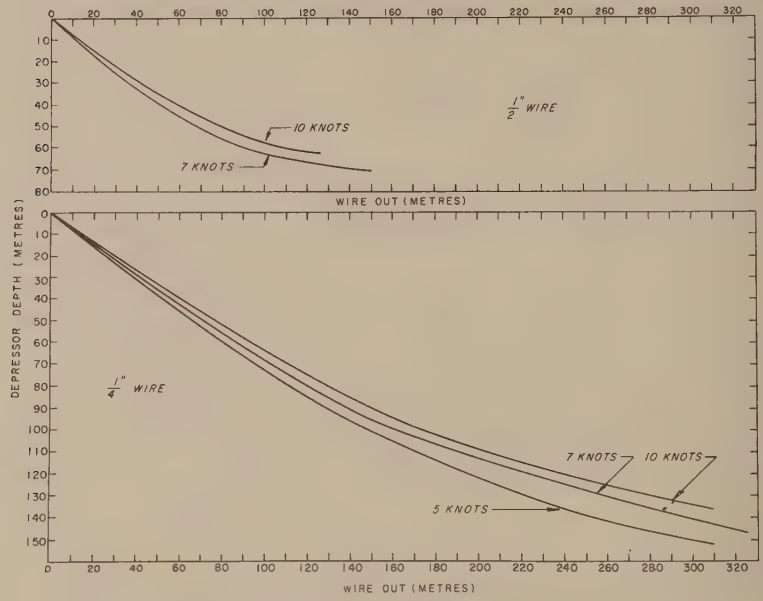

Figure 3. Relation of length of warp to depressor depth at various speeds.

at 10 knots. For $\frac{1}{2}$ inch wire the depressor depths were 40 and 60 m at a towing speed of 7 knots. These data, which are shown in Figure 4, have been plotted in terms of wire length (distance from terminal end) against depth rather than the distance of the depressor behind vessel against depth. Although such a plot does not show the actual curvature of the wire, it is more convenient for determining the proper spacing of samplers. For example, to sample at 60 m using $\frac{1}{4}$ inch wire at a towing speed of 7 knots and with the depressor at 150 m, the sampler should be positioned 142 m from the depressor. The total amount of wire out would be 343 m.

Results and Discussion

The multiplane kite-otter displays excellent diving and stability characteristics. The sensitivity of the turnbuckle adjustments for sheer is such that minute changes in towing angle are easily made. Adjustments for depth are not advisable. Once the final adjustments have been made, the sheer and diving characteristics remain constant so that the gear may be towed either from the side or from the stern of the vessel.

The maximum practical depressor depth varied more with wire size than with velocity. Because the relation of wire size to maximum depressor depth is inverse, it is desirable to use the smallest diameter wire practicable. It should be possible to use $^3/_{16}$ or $^7/_{32}$ inch diameter wire at speeds up to 7 knots and thereby increase the sampling depth appreciably.

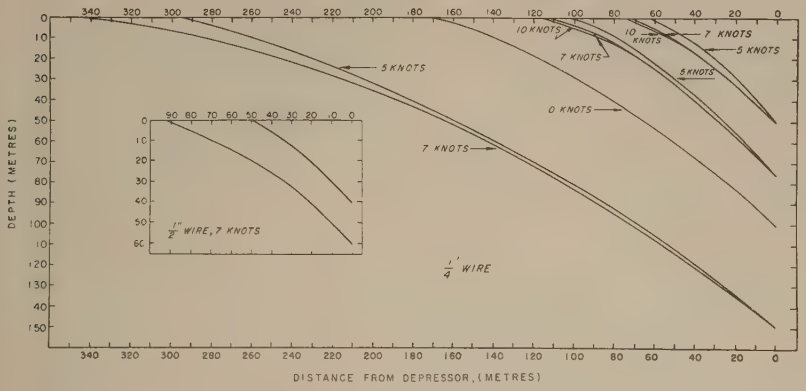

Figure 4. Curves for determining sampler spacing for $\frac{1}{4}$ inch wire with the depressor at 150 m (towing speed 5 and 7 knots), 100 m (towing speed 10 knots), 75 m (towing speed 5, 7, and 10 knots), and 50 m (towing speed 5, 7, and 10 knots) and for $\frac{1}{2}$ inch wire with the depressor at 40 and 60 m (towing speed 7 knots).

Because wire vibration makes the attachment of samplers difficult, it is more convenient to set out the gear and attach the samplers while stopped. The disadvantage of doing this is that the depth of water must be approximately twice that of the maximum desired sampling depth.

For most sampling, it appears that the 60 pound multiplane is the most practical size. We have, however, made up a half scale model weighing 25 pounds to be used with standard $^3/_{32}$ inch bathythermograph wire.

Because of the variations in ships' speeds and towing facilities, it would be advisable to undertake separate calibrations to meet specific needs.

The use of a small recording depth gauge that could be clipped onto the towing wire would greatly facilitate this work. A depth gauge would have the further advantage in that the wire profile could be calibrated with the samplers attached to the towing wire.

Summary

The multiplane kite-otter as a depressor is described. Depth and wire profile calibrations for a 60 pound multiplane and $\frac{1}{4}$ inch and $\frac{1}{2}$ inch towing wire at speeds of 5, 7, and 10 knots are presented. The diving and stability characteristics of the multiplane are discussed. Through the use of the multiplane kite-otter, it is possible to sample at high speed and at specific depths down to 150 m or more.

Reference

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A Quantitative Multiple Opening-and-Closing Plankton Sampler for Vertical Towing

By

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Introduction

The lack of standardization of plankton sampling equipment in present-day biological oceanography reflects the inherent problems involved in quantitative studies of organisms so diverse in size and structure as plankton. An investigator's choice of a suitable sampler necessarily depends upon such factors as the taxonomic group or groups to be studied (their concentration and size range), the depth and areal extents to be sampled, the type of research ship, the time and funds available. These factors in turn govern the size of the sampler (diameter of mouth opening, mesh diameter, length of net), the type of current meter and mechanical principle of the sampler.

In this article we describe a sampler for the investigation of the vertical distribution of planktonic organisms, which is of more complicated design but simpler in operation than those generally used for deep serial sampling. In serial sampling for bathypelagic organisms, several instruments need to be sent down in closed position and require a mechanism to open the nets at the desired depth levels and close again at others (Nansen, 1915; Juday, 1916; Kemp, Hardy, and Mackintosh, 1929; Leavitt, 1935; Clarke and Bumpus, 1950; Barnes, 1953; Currie and Foxton, 1957; Bogorov, 1958; Bary, *et al.*, 1958; etc.). Most of them operate most efficiently singly and some mechanical difficulty is encountered when a series of samplers are attached to the wire cable at successive intervals. The most serious problems encountered with such devices have been the failure of messengers to activate the release mechanisms of successively lower samplers and also the considerable time and effort required to attach to and detach from the wire cable a series of such instruments. Other devices used for serial sampling include the plankton pump (Gibbons

* Contribution from Lamont Geological Observatory, Columbia University, No. 369, Biology Program No. 26.

and Fraser, 1937; Wiborg, 1948), the plankton bar (Tonolli, 1951), and the continuous plankton recorder (Hardy, 1939). The first two were designed for quantitative sampling of comparatively shallow layers and are impractical for bathypelagic work in the ocean; the third instrument was designed for high-speed towing of near-surface water layers and filters relatively small amounts of water, making it unsuitable for some studies.

The need exists for a quantitative plankton sampler for deep-water sampling (below 400 m depth), that could take several uncontaminated samples at successive depth ranges (thus saving precious ship's time) and that would filter relatively large amounts of water. A vertical successive sampler of this nature has been built by Motoda (1953), using a single net (57 cm in mouth diameter). A cylindrical apparatus attached at the end contained five small store-nets that revolved into position, enabling five separate samples to be taken in one single haul.

The present sampler also has the ability to take multiple samples in one single haul, but employs different mechanical principles from that of Motoda. It was particularly designed to study the vertical distribution of planktonic Foraminifera and other small zooplankton, for which large volumes of water (50 m^3 or more) need to be filtered. With the scarcity of multiple plankton samplers, it is hoped that the present instrument may contribute to further progress in biological instrumentation.

Principles

The operation of the present sampler depends upon the following components:—

(a) four pivoting rods, having a common axis at one corner of the square frame (Fig. 1). Each plankton net is anchored to two adjacent pivoting rods; the two middle rods serve as common attachments for the first-and-second and second-and-third nets;

(b) elastic shock cords (elastic bands) attached to the frame and outwardly extending ends of the pivoting rods, are held under tension;

(c) restraining strings, tied from each of the inwardly extending ends of the pivoting rods through the release mechanism;

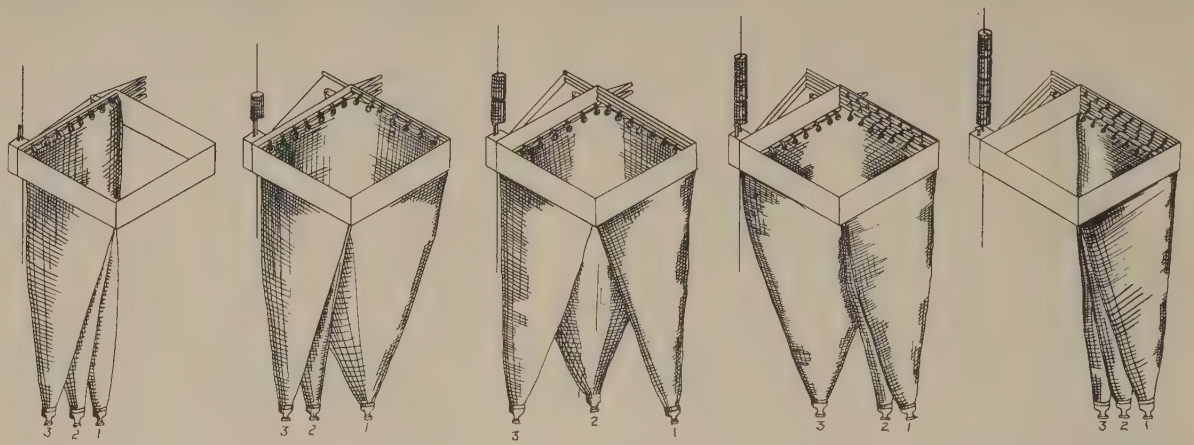
(d) cutting shaft on release mechanism.

At the start of the tow, all four pivoting rods are held (tied by strings) to the side of the release mechanism, while the three nets are folded and closed. The principle of multiple sampling by the present instrument is basically simple and involves three interdependent actions (Fig. 1):—

(a) a messenger hits the cutting shaft of the release mechanism, thus severing the string restraining the first pivoting rod (Note: downward movement of this shaft is controlled by friction applied by a tension screw and by bar-stops in the release mechanism), resulting in:—

(b) release of and 90° rotation of first pivoting arm, caused by rotational force applied by elastic shock cord at outwardly extending end of pivoting rod*, resulting in:—

* The mechanism of the pivoting rod operation is that of a class one lever.



Step 1
All nets closed. All shock cords taut. Cutting shaft on release mechanism at maximum height.

Step 2
First messenger hits. Cutting shaft severs string, thus releasing first pivoting rod and opening first net.

Step 3
Second messenger hits. Similarly, first net closes and second net opens simultaneously.

Step 4
Third messenger hits. Similarly, second net closes and third net opens simultaneously.

Step 5
Fourth messenger hits. The third and last net closes.

Figure 1. Simplified drawings of operation of the multiple plankton sampler. The depth-flowmeter with protective frame sides and the extention post for anchoring the cod-ends are not shown.

(c) opening of the first plankton net. Sufficient tension on the elastic shock cord keeps the pivoting rod firmly in its new position.

The second messenger activates these same three steps and simultaneously closes the first net and opens the second one. Similarly, the third messenger closes the second net and opens the third. The fourth messenger closes the third net. At the end of the tow, all four pivoting rods have rotated to the side adjacent to the release mechanism, while the three nets are closed and contain their plankton catches from three successive depth intervals.

Description of Materials and Mechanism

Frame (Fig. 2)

The face opening of the square frame is 55 cm by 55 cm, inside of which are mounted the three plankton nets. The frame walls are about 40 cm high and one cm thick, cut out at four sides for lightness and paneled with sheet aluminium. A canopy (1) is constructed along two sides (opposite the pivoting rods) to deflect the flow of water over the folded nets to prevent contamination. The instrument is attached to the wire cable at one corner of the frame through the release mechanism block and at the lower end of the extension post.

Four pivoting rods (2), 75 cm long, are mounted above each other on a common axis, which is located at one corner of the frame. The uppermost pivoting rod is 45 cm long inside the frame and extends 30 cm outside the frame. The lower rods are consecutively shorter by 0·6 cm to allow nesting of the closed nets.

Shock cords (elastic bands, 0·5 cm diameter and 50 cm length) are fastened through anchoring eyes at the outwardly extending portions of the pivoting rods and at the other end to anchoring eyes on the frame (3). Under tension the shock cords are guided over a roller bracket to prevent interference with the bar-stops (4).

Release mechanism (Fig. 3)

The release mechanism serves the dual purpose of triggering four separate opening-and-closing actions of the pivoting rods and of holding the wire. It also enables the sampler to rotate freely around the wire cable. The release mechanism block (5) has the general dimensions of 6 cm by 6 cm by 15 cm. One quarter section of this block is hinged for insertion of the wire cable into the vertical channel (6). A brass sleeve is placed at each end of the channel to reduce wear on the wire. A one-piece hand screw (7) is used to simplify locking the hinged block around the wire.

A stainless steel cutting shaft (8), 17 cm long and 1 cm diameter, is placed vertically within the release mechanism and is equipped with a knife blade (9); the blade is 5 cm above the bottom of the shaft. This spacing, as well as that between the four bar-stops and the four strings, is significant for the proper operation of the release mechanism.

A lateral tension screw (10) fitted with a teflon end applies sufficient friction to the stainless steel shaft to prevent premature downward travel under the weight of spent messengers. This friction enables the cutting shaft to support the combined weight of three messengers. Yet, a striking action applied by a messenger will force the shaft downward until halted by a bar-stop.

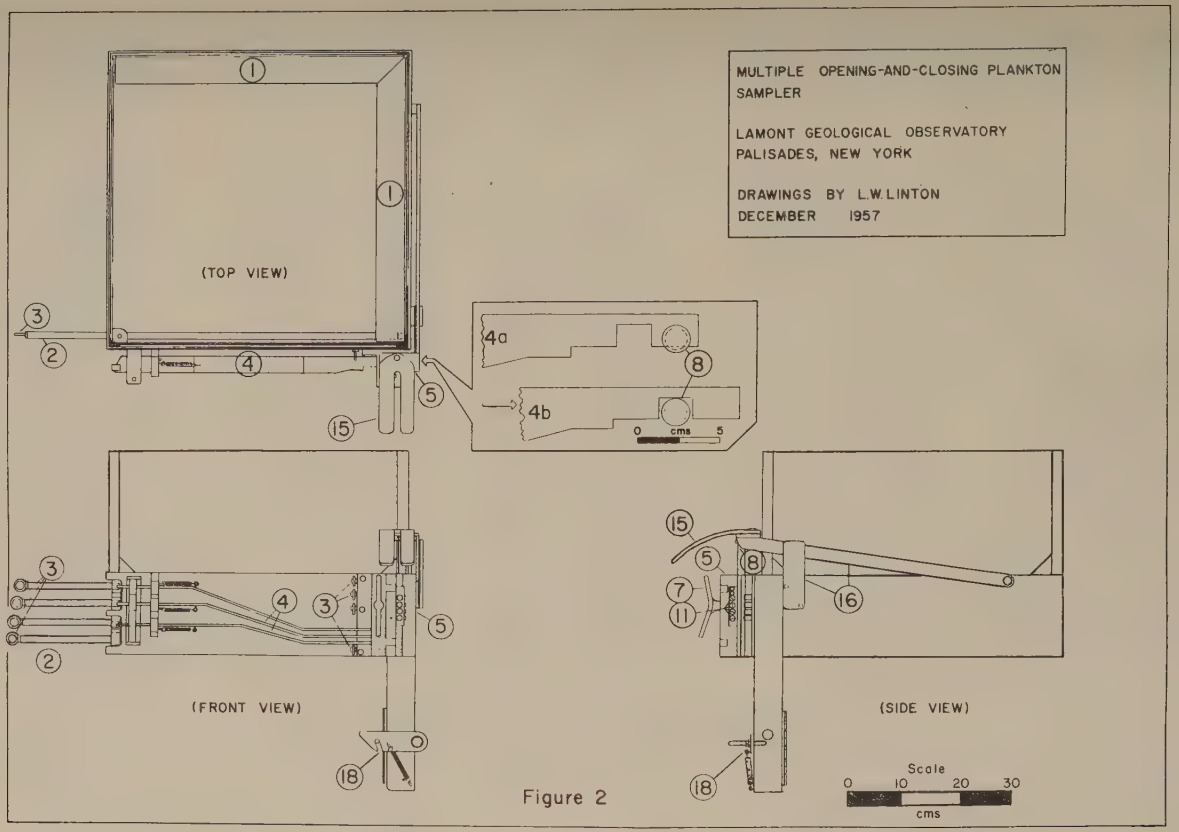


Figure 2. Schematic drawings of the multiple opening-and-closing plankton sampler. See key in Figure 3.

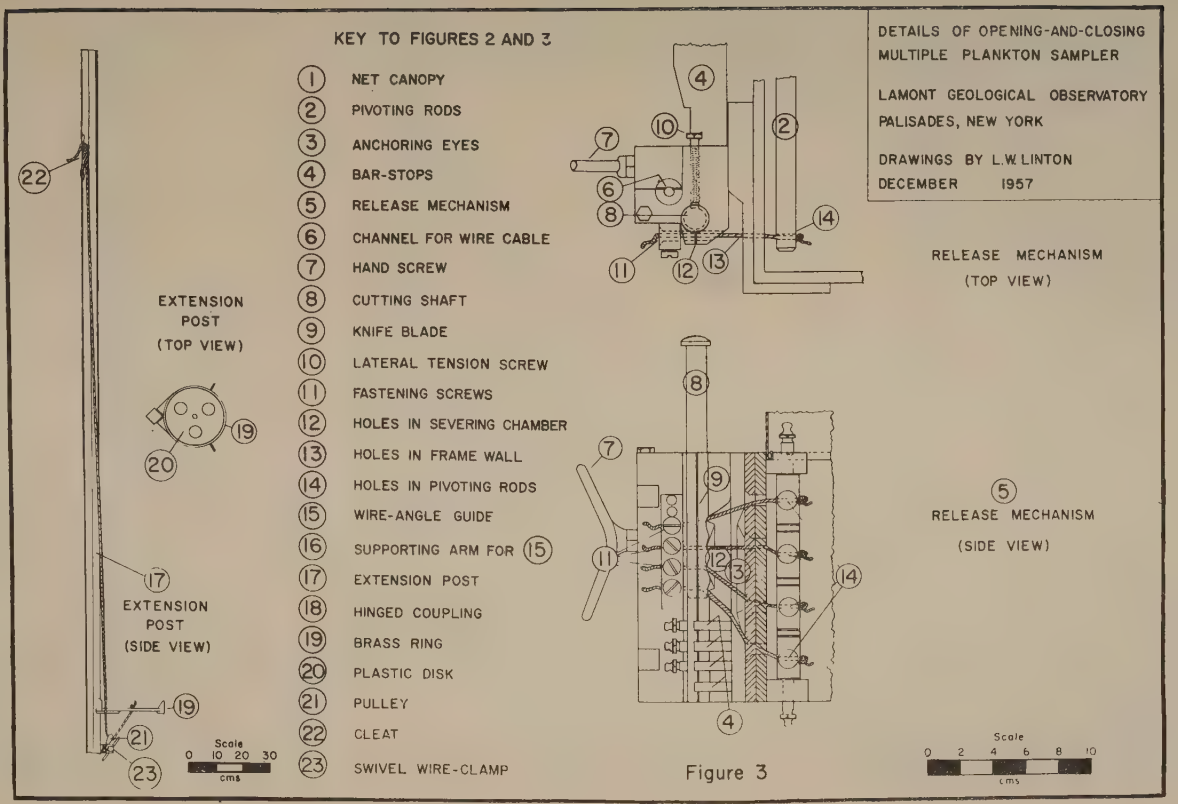


Figure 3. Schematic drawings of release mechanism and extention post.

The bar-stops (4) are 3 cm wide and are positioned adjacent to their corresponding pivoting rods. Nylon bumpers at the ends of the bar-stops serve to absorb the shock of the striking action of the pivoting rods. The other ends of the bar-stops are tapered to fit into the release mechanism and are shaped with appropriate slots (4a and 4b in Fig. 2 insert) to halt as well as to allow downward travel of the cutting shaft. Springs are provided to prevent the bar-stops from sliding forward prematurely. The brass bar-stops control the travel of the cutting shaft, permitting each of the four strings to be cut one at a time. The four strings hold the pivoting rods to the side of the release mechanism, while keeping the shock cords under tension. Severing the strings one at a time triggers the opening-and-closing action of the plankton nets. The sequence of rotating actions of the pivoting rods are utilized to strike and slide forward the bar-stops so that each of the slots are successively placed directly below the cutting shaft (see insert in Fig. 2).

The travel of the cutting shaft is controlled by (a) the striking action of a messenger, causing downward movement and severing of a string, (b) the blocking by a bar-stop, (c) friction applied by the lateral tension screw upon the cutting shaft, and (d) the placement of a slot in the bar-stop directly below the cutting shaft, allowing its further downward travel when a second messenger strikes. These four steps, including the pivoting action of the rod that simultaneously strikes and slides forward one bar-stop, represent one chain reaction that enables the opening-and-closing of one net. Subsequent messengers set off three similar actions.

Four series of holes were provided for threading the strings and aligning them at four critical positions: (a) fastening screws at the outer edge of the release mechanism (11); (b) severing chamber where cutting action of strings by knife blade takes place (12); (c) holes through frame and angle iron (13); and (d) holes through individual pivoting cords (14). The strings are tied at one end by the fastening screws (11) and at the other by knots at the pivoting rods.

A wire-angle guide (15) and supporting arm (16) rest upon the cutting shaft. The former consists of a fork-like extension which can swivel with changes in wire-angle and within which the wire rides. At large wire-angles it insures a proper downward action of the cutting shaft by a messenger.

Extension post (Figs. 2 and 3)

An extension post (17) is provided for stability of the instrument on the wire and is attached to the frame by a hinged coupling (18). This extension post consists of: (a) a box aluminium member (3 m in length); (b) a brass ring (19), 21 cm inside diameter, which is bolted to the lower extremity; (c) a plastic disk (20), 21 cm diameter, which is fitted into the ring for retaining the cod-ends in an orderly fashion. This disk is held in position by the downward pull of a rope, which runs through a pulley (21) and is attached to a cleat (22) above; and (d) a swivel wire clamp (23) which holds the wire in position at the lower end of the extension post.

Plankton nets

Three 200-micron mesh size (Nitex 202 or 86 meshes per inch) nylon nets were used, each having a 50 cm by 50 cm face opening. Each net consists of a

fore section, or nylon cloth collar about 50 cm long, a nylon filtering section 240 cm long, and a cod-end of nylon cloth 10 cm long — a total length of three metres.

The four sides of each plankton net are attached in the following manner: (a) One side is tied to one pivoting rod; (b) the adjacent side is tied to the next lower pivoting rod; and (c) the fold of the two remaining sides is anchored fast to the corner of the frame diagonally opposite the common shaft of the pivoting rods. The other two nets are secured in a similar fashion on the three lower rods.

Cod-ends

The plankton catches are collected in the cod-ends of the nets. Each cod-end is made of the upper half of a polyethylene bottle (10 cm diameter) and is clamped in an inverted position to the end of each plankton net. In this manner the plankton catch can be removed from the net by unscrewing the cap. The three cod-ends are fitted in the plastic disk, described under "Extension post."

Depth-flowmeter

The depth-flowmeter constructed at the National Institute of Oceanography in Great Britain according to the design of Currie and Foxton (1957) was used in the present sampler. This instrument is mounted inside the frame enclosure. It consists of a flowmeter, onto which has been mounted a Bourdon tube depth recording unit. The depth is recorded on a smoked glass cylinder and read by the vertical movement of a stylus arm which is connected through a twin strip flexure system to the Bourdon tube. The volume of water filtered is measured by the number of revolutions of the cylinder, which is linked to the rotor through a worm gear system. The instrument can be calibrated in a pressure vessel to determine the vertical displacement at various depths.

In the present sampler a teflon rod is attached to the Bourdon tube and extends downward in the path of the rotating pivoting rods. The striking action of the pivoting rod on the teflon rod vibrates the stylus arm — thus leaving a depth mark on the smoked glass cylinder. The smoked glass cylinder is later removed and sprayed with a clear lacquer for protection. The traces on the smoked glass cylinder can be photographed by wrapping photographic paper about the cylinder and exposing it from within with a small light. The paper is developed and fixed, resulting in a permanent record of the volume of water filtered during the under-water travel of the instrument.

Field Operation

This instrument (Fig. 4) was tested initially in the Hudson Canyon area off New York on R/V "Vema" of the Lamont Geological Observatory in November 1957. Although the mechanical workings proved successful, more improvements and refinements were made for greater ease in shipboard handling. Further field testing was done in Bermuda waters on R/V "Panulirus" of the Bermuda Biological Station in May 1958. Five successful hauls were made. At the present time, the instrument is designed for vertical towing, but it can be modified for oblique towing. It is proposed that a future modification may be the use of a series of Bourdon tubes to trigger the opening-and-closing actions of the nets.

Figure 4. Multiple plankton sampler with first net open, as shown by position of first pivoting rod.

This may have the advantage of reducing the weight of the present sampler and allowing bridle attachment to the wire for oblique towing.

The procedure of handling the instrument during field testing was as follows:

Placing sampler on wire

1. The wire cable (5/32″) is inserted into release mechanism (6) and wire-angle guide (15). Door of release mechanism is locked by hand screw (7). Entire sampler can swivel freely.

2. A clamp is fastened to wire directly underneath release mechanism to prevent downward slippage of sampler.

3. The three-metre extension post (17) is connected to the sampler frame through hinged coupling (18). It avoids twisting of wire caused by corner mounting of the relatively heavy sampler.

4. The swivel wire-clamp (23) at the lower part of extension post is connected onto wire, allowing free rotation.

5. Directly above and below the lower part of extension post two wire-clamps are fastened to prevent downward or upward slippage of the entire plankton sampler.

6. The three cod-ends are mounted on a plastic disk (20) at the end of the extension post.

Triggering of device

1. Cutting shaft (8) is raised to maximum height so that the knife blade is ready to sever strings. Tension screw (10) is tightened to maximum friction on cutting shaft. The friction applied to the cutting shaft by the tension screw enables the former to remain stationary until a further downward action is applied by a second messenger.

2. All three nets are initially closed when the four rods (3) are held against frame wall (side of release mechanism). This is done by threading marlin strings through three series of holes (12, 13, and 14) and tying them to the ends of the bars in the release mechanism and holding them in position by fastening screws (11). The plankton sampler is now ready for lowering.

The plankton hauling operation

1. At the maximum desired depth of tow, the first messenger is sent down and causes the cutting shaft to sever the first string. Consequently, a 90° rotation of the first pivoting rod opens the first net and also records the depth on the depth-flowmeter.

2. A vertical tow is made while the depth-flowmeter continuously records the volume of water filtered on the rotating smoked glass cylinder.

3. At the end of the first depth interval sampled, a second messenger is sent down which closes the first net and simultaneously opens the second net.

4. At the end of the second depth interval sampled, a third messenger is sent down which closes the second net and simultaneously opens the third net.

5. At the end of the third depth interval sampled, a fourth messenger closes the third and last net.

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We wish to thank S. Harrison for constructing the instrument and his participation in its field testing. Helpful advice was given by A. Ludas, R. J. Menzies, A. Roberts, and J. L. Worzel of the Lamont Geological Observatory during the phases of innovating, constructing, and testing this sampler.

The depth-flowmeter incorporated in the present plankton sampler was designed by R. I. Currie and P. Foxton of the National Institute of Oceanography, Wormley, England.

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Summary

A quantitative, multiple plankton sampler is described which enables the sampling of plankton of three depth layers in a single, vertical haul. The device operates on the principle of opening-and-closing actions of three separate plankton nets. The nets are attached to four pivoting rods, having a common axis of rotation. At the start of the tow, the nets are folded to one side of the sampler frame. Messengers are used — one at a time — to activate each 90° rotation of the pivoting rods, thus enabling the opening-and-closing actions of the folded nets. At the end of the tow, the three nets are folded to the adjacent side of the frame. The rotation of the pivoting rods is accomplished by means of shock cords (elastic bands).

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Estimation of Growth Parameters for Data at Unequal Time Intervals

By

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If data on size (length) at age are available at equal time intervals, the usual methods, e. g., the Ford/Walford plot (WALFORD, 1946; BEVERTON and HOLT, 1957) can be used to estimate the parameters of VON BERTALANFFY's growth equation. Such methods cannot be applied directly if the data are at unequal intervals, e. g., data from the recapture of marked fish, some crustacean growth data and some results of fish rearing. These data can, however, be used to obtain similar plots giving estimates of the growth parameters, by the method described below.

With the usual notation, let the length of a fish at time t be given by

$$l_t = L_\infty \, (1 - e^{-K(t - t_0)})$$

and after a time interval, a, the length will be

$$l_{t+a} = L_\infty \, (1 - e^{-K(t-t_0+a)})$$

Then the growth increment, ${}_ay$, during time, a, will be

$$\begin{aligned} {}_ay = l_{t+a} - l_t &= L_\infty \, [(e^{-K(t-t_0)} - e^{-K(t-t_0+a)})] \\ &= L_\infty \, e^{-K(t-t_0)} \, (1 - e^{-Ka}) \end{aligned}$$

and the growth per unit time $= y$

$$= L_\infty \, e^{-K(t-t_0)} \, \frac{1 - e^{-Ka}}{a} \qquad \ldots\ldots(1)$$

The mid-point of the length interval is $\frac{1}{2}(l_t + l_{t+a})$ and will be denoted by x where

$$\begin{aligned} x &= \tfrac{1}{2} L_\infty \, (2 - e^{-K(t-t_0)} - e^{-K(t-t_0+a)}) \\ &= L_\infty \, [1 - \tfrac{1}{2} e^{-K(t-t_0)} \, (1 + e^{-Ka})] \\ L_\infty \, e^{-K(t-t_0)} &= 2 \, (L_\infty - x)/(1 + e^{-Ka}) \qquad \ldots\ldots(2) \end{aligned}$$

Substituting in equation (1), we have

$$y = (L_\infty - x) \cdot \frac{2(1 - e^{-Ka})}{a(1 + e^{-Ka})}$$

or, putting $\frac{1}{2}Ka = b$

$$\begin{aligned} y &= (L_\infty - x) \, K \frac{(1 - e^{-2b})}{b(1 + e^{-2b})} \\ &= K \, (L_\infty - x) \cdot \frac{\tanh b}{b} \qquad \ldots\ldots(3) \end{aligned}$$

Thus if for growth during a fixed duration of time, a, we plot y, the increment per unit time, against x, the mid-point of the corresponding length interval, the points will lie on a straight line cutting the x-axis at $x = L_\infty$ and having slope $-K \cdot \frac{1}{b} \tanh b$. If we plot points for time intervals of differing duration the points will lie on different lines, having the same x-intercept (L_∞) but having different slopes. However, the value of $b/\tanh b$ for small b is very close to 1 (see table) so that to a close approximation all points for a small b (small time interval) will lie on a line, intercept L_∞, slope $-K$.

As may be seen from the table, for values of b up to 0·4 the error is only 5% and these values of b will include most intervals likely to occur, e. g., for plaice, *Pleuronectes platessa*, $K = 0{\cdot}1$, $b = 0{\cdot}4$ for 8 years interval, for the Chub mackerel, *Rastrelliger* spp. $K = 0{\cdot}6$, $b = 0{\cdot}4$ for an interval of 1·3 years. If some of the time intervals in the data are very long, the method can still be used, if estimates of K can be obtained from part of the data where time intervals are either equal or relatively short. That is, for the long intervals we plot not the growth increment per unit time, y, but $y \cdot \frac{b}{\tanh b}$, where b is obtained from our first approximation to K. The values of the correction factor $b/\tanh b$ for b from 0 to 5 are given in the table. It will be seen that these points can be added to the graph to give the second approximation without having to replot the points for small time intervals.

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Table of $\frac{X}{\tanh X}$ (from X = 0·000 to X = 5·000)

(Derived from tables of *tanh X* as given in »Chambers' Six-Figure Mathematical Tables« by L. J. Comrie, Vol. II. Natural Values. (1949)

x	0	1	2	3	4	5	6	7	8	9	Mean proportional parts 1	2	3	4	5	6	7	8	9
0	1·0000	1·0000	1·0001	1·0003	1·0005	1·0008	1·0012	1·0016	1·0021	1·0027									
1	1·0033	0040	0048	0056	0065	0075	0085	0096	0108	0120	Mean differences not sufficiently accurate								
2	1·0133	0147	0161	0176	0191	0207	0224	0242	0260	0279									
3	1·0298	0318	0339	0360	0382	0405	0428	0452	0477	0502									
4	1·0528	0554	0581	0609	0637	0666	0696	0726	0756	0788									
5	1·0820	0852	0885	0919	0954	0989	1024	1060	1097	1134									
6	1·1172	1211	1250	1289	1329	1370	1411	1453	1496	1539	4	8	12	16	21	25	29	33	37
7	1·1582	1626	1671	1716	1762	1808	1855	1902	1950	1999	5	9	14	19	23	28	33	37	42
8	1·2048	2097	2147	2197	2248	2300	2352	2404	2457	2511	5	10	16	21	26	31	36	41	47
9	1·2565	2619	2674	2729	2785	2841	2898	2956	3014	3072	6	11	17	23	28	34	40	45	51
0	1·3130	3189	3249	3309	3370	3431	3492	3554	3616	3678	6	12	18	24	31	37	43	49	55
1	1·3741	3805	3869	3933	3998	4063	4128	4194	4260	4327	6	13	19	26	33	39	46	52	59
2	1·4394	4462	4530	4598	4667	4736	4805	4875	4945	5015	7	14	21	28	35	42	48	55	62
3	1·5086	5157	5229	5301	5373	5445	5518	5591	5665	5739	7	14	22	29	36	44	51	58	65
4	1·5813	5887	5962	6037	6113	6189	6265	6341	6418	6495	7	15	23	30	38	46	53	61	68
5	1·6572	6649	6727	6805	6884	6962	7041	7120	7200	7280	8	16	24	32	39	47	55	63	71
6	1·7360	7440	7521	7601	7682	7764	7845	7927	8009	8091	8	16	24	33	41	49	57	65	73
7	1·8174	8257	8340	8423	8506	8590	8674	8758	8842	8927	8	17	25	33	42	50	59	67	75
8	1·9011	9096	9781	9267	9352	9438	9524	9610	9696	9783	9	17	26	34	43	52	60	69	77
9	1·9870	1·9956	2·0043	2·0131	2·0218	2·0306	2·0394	2·0481	2·0570	2·0658	9	17	26	35	44	53	61	70	79
0	2·0746	2·0835	0924	1013	1102	1191	1280	1370	1460	1549	9	18	27	36	45	54	63	71	80
1	2·1639	1730	1820	1910	2001	2091	2182	2273	2364	2456	9	18	27	36	45	54	64	73	82
2	2·2547	2638	2730	2822	2914	3006	3098	3190	3282	3375	9	18	28	37	46	55	64	74	83
3	2·3467	3560	3652	3745	3838	3931	4025	4118	4211	4305	9	19	28	37	47	56	65	74	84
4	2·4398	4492	4586	4680	4774	4868	4962	5056	5150	5245	9	19	28	38	47	56	66	75	85
5	2·5339	5434	5528	5623	5718	5813	5908	6003	6098	6193	9	19	28	38	47	57	66	76	85
6	2·6288	6384	6479	6575	6670	6766	6862	6957	7053	7149	10	19	29	38	48	57	67	77	86
7	2·7245	7341	7437	7533	7629	7726	7822	7918	8015	8111	10	19	29	39	48	58	67	77	87
8	2·8208	8304	8401	8498	8595	8691	8788	8885	8982	9079	10	19	29	39	48	58	68	77	87
9	2·9176	2·9273	2·9370	2·9468	2·9565	2·9662	2·9759	2·9857	2·9954	3·0052	10	19	29	39	49	58	68	78	88
0	3·0149	3·0247	3·0344	3·0442	3·0539	3·0637	3·0735	3·0833	3·0930	3·1028	10	20	29	39	49	59	68	78	88
1	3·1126	1224	1322	1420	1518	1616	1714	1812	1910	2008	10	20	29	39	49	59	69	78	88
2	3·2107	2205	2303	2401	2500	2598	2696	2795	2893	2991	10	20	29	39	49	59	69	79	88
3	3·3090	3188	3287	3385	3484	3583	3681	3780	3878	3977	10	20	30	39	49	59	69	79	89
4	3·4076	4175	4273	4372	4471	4570	4668	4767	4866	4965	10	20	30	40	49	59	69	79	89
5	3·5064	5163	5262	5361	5460	5559	5658	5757	5856	5955	10	20	30	40	50	59	69	79	89
6	3·6054	6153	6252	6351	6450	6549	6648	6748	6847	6946	10	20	30	40	50	59	69	79	89
7	3·7045	7144	7244	7343	7442	7542	7641	7740	7839	7939	10	20	30	40	50	60	70	79	89
8	3·8038	8137	8237	8336	8436	8535	8634	8734	8833	8933	10	20	30	40	50	60	70	80	89
9	3·9032	9131	9231	9330	9430	9529	9629	9728	9828	9927	10	20	30	40	50	60	70	80	90
0	4·0027	4·0126	4·0226	4·0325	4·0425	4·0525	4·0624	4·0724	4·0823	4·0923	10	20	30	40	50	60	70	80	90
1	4·1023	1122	1222	1321	1421	1521	1620	1720	1820	1919	10	20	30	40	50	60	70	80	90
2	4·2019	2119	2218	2318	2418	2517	2617	2717	2816	2916	10	20	30	40	50	60	70	80	90
3	4·3016	3116	3215	3315	3415	3514	3614	3714	3814	3914	10	20	30	40	50	60	70	80	90
4	4·4013	4113	4213	4313	4412	4512	4612	4712	4812	4911	10	20	30	40	50	60	70	80	90
5	4·5011	5111	5211	5311	5410	5510	5610	5710	5810	5909	10	20	30	40	50	60	70	80	90
6	4·6009	6109	6209	6309	6409	6509	6608	6708	6808	6908	10	20	30	40	50	60	70	80	90
7	4·7008	7108	7208	7307	7407	7507	7607	7707	7807	7907	10	20	30	40	50	60	70	80	90
8	4·8006	8106	8206	8306	8406	8506	8606	8706	8806	8906	10	20	30	40	50	60	70	80	90
9	4·9005	9105	9205	9305	9405	9505	9605	9705	9805	9905	10	20	30	40	50	60	70	80	90
0	5·0005																		

The Scientific Name of the Common Cod

By

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Anyone using the voluminous literature on the common cod of the Atlantic Ocean soon becomes aware of inconsistency in the scientific nomenclature applied to this species. The purpose of this paper is to point out the causes of confusion and to indicate the proper name to be used under the International Code of Zoological Nomenclature.

In the 10th edition of the *Systema Naturae* (the starting point of formal zoological nomenclature), LINNAEUS described the genus *Gadus* on page 251. Following this description there are brief descriptions of 15 species which LINNAEUS placed in *Gadus*. At the top of page 252 is species number 2 — *callarias*, from European and Baltic seas. Directly beneath *callarias* on the same page is species number 3 — *morhua* (changed to *morrhua* by many later authors) from European seas. Both *G. callarias* and *G. morhua* were recognized as valid species until 1838 when FRIES (in FRIES, EKSTRÖM and SUNDEVALL, 1836–48) realized that the two names were applied to the same species. The name *G. callarias* had been used for young specimens and for the stunted population in the Baltic, while adults had been called *G. morhua*.

When two names apply to the same species, only one has priority, and it is this name alone which may validly be used for the species. The other name becomes a synonym, though as we shall see, it still remains available for use. In most instances of this nature there is little difficulty in determining priority. It is simply a matter of picking the first properly proposed name. In the case of the cod, however, the names *callarias* and *morhua* appear not only in the same volume, but on the very same page, and it is this fact which is the root of the difficulty.

The International Rules of Zoological Nomenclature state that when two species of the same date are united to form a single species, the name selected by the first reviser shall apply as the name of the species. It is recommended, however, that the name which occurs first in the publication be chosen if possible. FRIES was the first to synonymize *morhua* and *callarias* and is thus the first reviser. He chose the name *morrhua*, and although he did not apply the principle of page precedence, his choice is valid under the present rules.

It was, however, long ago realized that an additional measure of stability was necessary for the names of certain animals, and APSTEIN (1915) published a list of *nomina conservanda*, names which he felt should be conserved regardless of priority. Included in the *Pisces* section of his list was the genus *Gadus* and the species *morrhua*. Although the International Commission on Zoological Nomenclature (1922, Opinion 74) ruled they could not adopt APSTEIN's list *en bloc*, they were prepared to consider his suggestions one at a time, and later in the same year (Opinion 77) and with the recommendation of DAVID STARR JORDAN, the Commission followed APSTEIN's suggestions with regard to *Gadus* and other names and placed them on *The Official List of Generic Names in Zoology*. In 1956 the Commission (HEMMING, 1956) placed the name *morhua* LINNAEUS 1758, as published in the combination *Gadus morhua* on *The Official List of Specific Names in Zoology* (species no. 1079).

The Commission had previously decided (HEMMING, 1950) that once a specific name is placed on *The Official List of Specific Names in Zoology* this name is to be used in preference to any other name, even if it is found not to be available or not the oldest name for the species; unless the Commission directs otherwise.

There is no doubt, therefore, that *Gadus morhua* (note the use of LINNAEUS' original spelling of the specific name) is the proper scientific name of the cod. This conclusion would follow automatically by application of The International Rules of Zoological Nomenclature (as they stand when this is being written, May, 1959). The name is further reinforced by its inclusion in *The Official List of Specific Names in Zoology*, and should the rules change from "the rule of the first reviser" to "the rule of page precedence", the name *morhua* would still remain valid.

It is of interest to note that although the name *callarias* is a synonym of *morhua* in the genus *Gadus*, *callarias* is still available for use, and SVETOVIDOV (1948) has recognized the Baltic population of cod as the subspecies *Gadus morhua callarias*.

Acknowledgement

I thank Mr. JOHN P. WISE of the U. S. Fish and Wildlife Service for his kindness in commenting on the manuscript.

Summary

1. The original descriptions of *Gadus callarias* and *Gadus morhua* first appeared on the same page. When it was realized that the two names applied to the same species confusion arose as to which name should properly be used.

2. The International Commission on Zoological Nomenclature placed *Gadus* on *The Official List of Generic Names in Zoology* and *morhua*, as published in the combination *Gadus morhua*, on *The Official List of Specific Names in Zoology*. They also decided that once a specific name is placed on the *List* it is to be used in preference to any other name, even if it is found not to be available or not the oldest name for the species; unless the Commission otherwise directs. The scientific name of the common cod should therefore stand as *Gadus morhua* Linnaeus 1758.

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Whiting Tagging: How the Tag Return Rate is Affected by the Condition of Fish when Tagged

By

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Introduction

In November and December 1957, 6,200 whiting and nearly 500 other fish were tagged and released in the north-western part of the Irish Sea off the coasts of Eire and Northern Ireland, where there is a substantial winter seine net and trawl fishery for whiting. During the seven months immediately after the tagging 952 of the tagged fish were recaptured. While it is too soon to draw conclusions about factors such as fishing mortality or migration patterns (and no attempt is made here to analyse the first results from such viewpoints) it is possible to use the results already to hand to illustrate how, and to what extent, the return of tagged fish is affected by some of the factors in the tagging technique and procedure.

Methods

The fish were caught at 20–30 fm in a whiting seine which had a cotton cod-end of approximately 70 mm mesh. The gear was fished by the usual Danish (or anchor) method and 6 to 7 coils of rope a side were used. The time taken for shooting was about 15 minutes, and for hauling about 45 minutes. The fish were brought on deck in the usual manner and were at once picked up and placed in tanks with a continuous circulation of water; lowering the fish directly into the tanks was not practicable because of the quantity of rubbish which fouled the tank.

The tag used was a yellow plastic flag, 42 mm by 10 mm, of the type currently used for gadoid fish by the Lowestoft Laboratory, having a message in English on one side and French on the other, and attached through the back of the fish between the first and second dorsal fins by a loop of soft braided nylon, threaded through the body by means of a fine surgical needle (see Fig. 1).

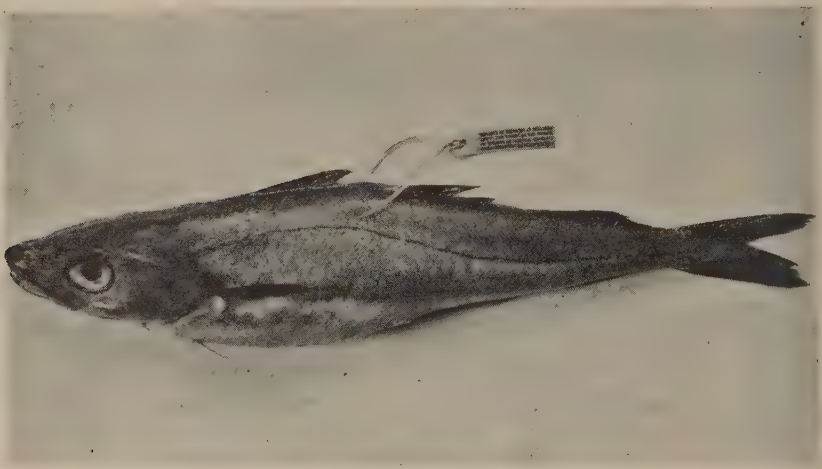

Figure 1. Photograph of a tagged whiting, overall length 31 cm.

As the fish were tagged they were graded according to their general liveliness and the condition of their scales. In the tanks most of the fish floated belly-up with distended swimbladders, but some, presumably with burst swimbladders, swam comfortably at the bottom of the tank. Those that floated were classified as Active (A) if, when disturbed, they succeeded in swimming below the surface for a few moments before floating again, and as Sluggish (B) if they made only rather feeble and ineffective attempts to swim down. Those swimming at the bottom of the tank were classified as Sinkers (S). Fish were graded into three catagories of scale condition; Good (G) if they were undamaged or had only a few scratches, Moderate (M) if up to about 5 sq. cm of scales had been removed or noticeably disturbed, and Poor (P) if the scale damage was more extensive. In practice, when there was a large number of fish in the tanks and tagging had to be done quickly, precise distinction between the A and B classifications was difficult, but for the most part grading could be done reasonably well. In most hauls there were a few fish that were rejected altogether because they were too badly damaged to be worth tagging.

Following the technique used for whiting by Danish workers in the North Sea, and earlier for cod in the Arctic by Trout, the tagged fish were released from a cage well below the surface of the sea. This procedure was adopted not only for all fish in categories A and B but also for most of those in category S, since although most of the latter were able to swim down of their own accord if released at the surface, they were not always able to do so soon enough to avoid being attacked by gulls. Immediately after being tagged, about twenty fish at a time were placed in a nylon mesh cage, about $40 \times 40 \times 60$ cm, which was lowered to a depth at which the swimbladder was sufficiently compressed to enable the fish to swim down when released. It was found by trial that the depth required for this was in the region of 15 fm, although even at this depth a fish occasionally floated to the surface again or failed to get out of the cage.

Table 1

Liberation and recaptures of whiting

Scale condition	Floaters		Sinkers	Total
	Lively (A)	Sluggish (B)	(S)	
Good (G)	84/376 } 22·3%	163/905 } 18·1%	68/241 } 28·0%	315/1522 } 20·7%
Moderate (M) ...	54/345 } 15·7%	297/1867 } 15·9%	71/556 } 12·8%	422/2768 } 15·4%
Poor (P)	15/189 } 7·9%	91/1223 } 7·4%	26/498 } 5·2%	132/1910 } 6·9%
Total	153/910 } 16·8%	551/3995 } 13·8%	165/1295 } 12·7%	869/6200 } 14·1%

Results

Up to the 1. July 1958, out of the 6,200 whiting tagged 869 tags had been returned; the sources of these returns were: Northern Ireland 512, Eire 209, France 80, England 35, and Scotland 11, with a further 22 caught by vessels whose nationality was not reported. The recaptures, classified according to condition when tagged, are given in Table 1, which shows for each category the number tagged (lower figure), the number returned (upper figure), and the percentage recaptured.

These data have not yet been subjected to a rigorous statistical analysis, but certain features are evident from inspection. Thus the blown or unblown condition of the fish (A, B, or S) does not seem to have had a very marked effect, although the total recaptures of condition A fish show a little higher percentage recapture than do those of B and S fish. In contrast, the effect of scale damage was considerable, the percentage recapture (7%) of fish with poor scales being only one-third of that (21%) of fish with good scales, while that (15%) of fish having moderate scales was intermediate.

Discussion

Clearly, the differences between the percentage returned of the various categories of fish must be due mainly to mortality arising from tagging. Whether many of even the best fish died through being caught and tagged cannot be established directly, but if it is supposed that all fish of the category giving the best returns ((S), good scales, 28%) did in fact survive, then at least something like $100 - (5{\cdot}2/28 \times 100) = 81\%$ of the category giving the worst returns ((S), poor scales, 5·2%) must have died. The fact that it is the degree of scaling rather than the swimming ability of the fish which seems to be the critical factor does perhaps indicate that the tagging mortality among the best fish may not be very high, because many of the fish classified as having "good" scales were virtually unmarked. If it had been that blown or swimming condition (A, B, or S) was the more important, the same kind of conclusion would not necessarily follow, because this classification is much less clear-cut than that of scaling and there is no way of knowing whether all fish of condition A, for example, are really as viable as they might appear to be.

Table 2

Number of fish tagged and recaptured of species other than whiting

Species	Tagged	Recaptured	% Recaptured
Cod	106	56	53%
Haddock	67	9	13%
Saithe	4	1	25%
Hake	242	15	6%
Dogfish	75	2	3%

We can also use the data for other species to give a comparison. During the work several other species were tagged with the same kind of tag; the details are given in Table 2. Mortality at tagging, as judged by condition when tagged and liability to surface after release, could well have been very high for hake, but probably negligible for cod. This impression is supported by the percentage recaptures for these two species. The very low percentage of dogfish recaptured is interesting, since these appeared to be particularly robust and little affected by capture or tagging. It is dangerous to build too much on a comparison between species which can differ both in their liability to capture by the gear and also in their movements into and out of the fishing area, but the 53% returns of cod suggest that even the 28% returns of the best quality whiting may be an underestimate, particularly as during most of the time the fishing fleet was concentrating on whiting rather than cod. This has the corollary that the mortality at tagging of even these whiting may be appreciable, perhaps around 50%.

There thus remains some doubt as to the percentage of whiting that would have been recaptured had there been no tagging mortality, but the indications are that it is probably within the limits of 28% and 53%. In contrast, the overall recapture rate of whiting unclassified by condition or scales is 14%, and the difference between these estimates is witness to the value of careful recording of the condition of the fish when tagging. To what extent it would be possible to use objective systems of condition classification for the tagging of species other than whiting would need further investigation, but the results reported here indicate that where such a system can be devised it would give a worthwhile improvement in the information obtainable by the tagging method.

It is as yet too early to discuss the implications of the results in relation to questions of regulation but, in passing, it is worth noting that even 28% is a very high recapture rate for a period of only 7 months after tagging and indicates that the influence of fishing on the stock is probably large. The extent of this influence will depend upon the pattern of movement during and after the season, and it may well differ on fish of different sizes. Some idea of the extent of movements of tagged whiting is given by Figures 2 and 3. Although the great majority of recaptures have come from within the area of the Northern Ireland fishery, some migration evidently occurs, particularly to the eastern part of the Irish Sea.

Acknowledgement

The assistance in the arrangement and conduct of the experiment given by Mr. K. U. Vickers of Northern Ireland, and Dr. A. E. J. Went and Dr. F. A. Gibson of Eire is gratefully acknowledged.

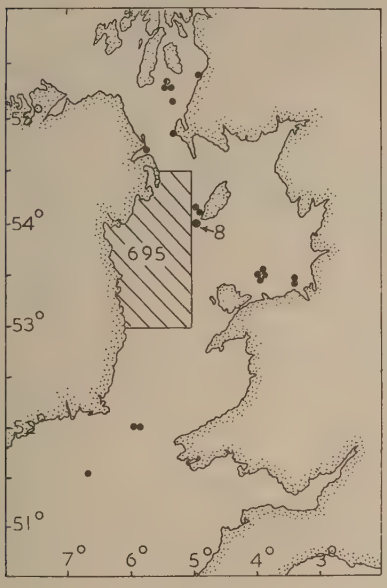

Figure 2.

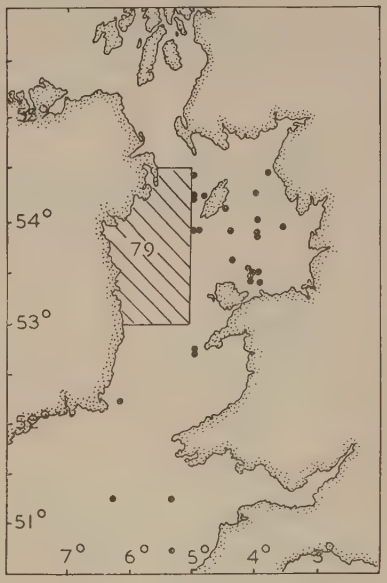

Figure 3.

Figure 2. Positions where tagged whiting were recaptured within 100 days of tagging. (The cross-hatching shows the general tagging area, and the figure within it indicates the number recaptured in that area.)
Figure 3. Positions where tagged whiting were recaptured 100–210 days after tagging.

Summary

1. A technique is described of classifying the condition of whiting when being tagged. The influence of condition on the rate of recapture is shown from an experiment in which 6,200 whiting were tagged in the Irish Sea, November–December 1957, and from which 869 (14·1 %) were recaptured within 7 months of liberation.

2. The fish were graded on tagging according to whether they floated or swam down in the marking tanks, whether the floaters were lively or sluggish, and according to the extent of scale damage.

3. The extent to which fish were blown or could swim did not greatly affect returns, but the extent of scale damage certainly did. Returns from fish with scales in good condition were three times those from fish with extensively damaged scales. The highest percentage of returns (28 %) came from the category of fish which swam down in the tanks and had scales in good condition.

4. The implications of these results to questions of the estimation of the true fishing rate and of the mortality due to tagging are discussed. It is concluded that where an objective system of condition classification can be devised it may materially enhance the value of the information obtained from the tagging experiment.

A Method of Analysis of some Tagged Haddock Returns

By

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Introduction

One fact that emerges from an analysis of tag returns is that tagged fish do not all move in the same way. Haddock tagging, for example, has shown that returns may come from the position of liberation after a very long period of freedom, or from a long way off after a comparatively short time. In some experiments such variations are extremely large, and it may even appear as if the fish are moving entirely at random. This is an extreme case. The opposite extreme is exhibited by a species such as herring, in which the individuals often move as a single unit in shoal formation.

There is no reason to suppose that haddock move in shoals as herring do and, as a first approximation, it seems reasonable to imagine that the movement of a haddock at any instant is the resultant of two components: (a) a group, or directional tendency, that measures the average rate of movement of the whole "group" in a particular direction (in this context, "group" could mean anything from a number of tagged fish to the entire fish population, according to circumstances) and (b) an undirected or random component that measures the way in which the movement of any individual at any instant departs from the overall directional average.

If (a) is large and (b) is small, the fish will move comparatively rapidly in a particular direction. If (a) is small and (b) is large, the individuals will disperse, possibly to a sufficient extent to mask their mean direction of travel.

In the following pages, an attempt has been made to analyse some haddock tag returns in terms of these two components.

Experimental Details

Several haddock taggings have been made and a summary of some of these experiments is given below:—

Date	Position		Number liberated	Number returned by Jan. 1959	Type of tag
June 1956	Findon Ness (North Sea)	B13d	240	33 (14%)	Lea hydrostatic
May 1957	Bell Rock	B11b	989	224 (23%)	Yellow plastic tag
Nov./Dec. 1957 .	Bell Rock (North Sea)	B11b	377	55 (15%)	Yellow plastic tag

Figure 1. Distribution of 224 haddock returned out of 989 liberated in May 1957 off Bell Rock. Circle indicates point of liberation. Numerals indicate number of days between liberation and recapture of each fish. Lines indicate approximate direction and distance travelled by each fish.

All tags were attached by nickel or stainless steel wire (23 S.W.G.) through the dorsal musculature of the fish, just in front of the first dorsal fin. The yellow plastic flags used in the last two experiments were made of 95% clear polythene and 5% yellow polythene. These tags were manufactured in two flattened halves, which were subsequently sealed together with a numbered paper inside.

The majority of fish tagged were two year-olds and about 30 cm in length when liberated.

Results

The largest number of returns came from the May 1957 experiment in which 989 haddock were caught and liberated from a commercial small line boat working near the Bell Rock, St. Andrews Bay. By the end of January

1959, 224 of these fish had been returned, and their positions of liberation and recapture, connected by straight lines, are shown in Figure 1. These returns can be divided into two groups: (a) up to the middle of November 1957 (about 180 days absence) recaptures were distributed around the position of liberation in what may loosely be called a "random" manner, and (b) after the middle of November, and especially in January and February (about 250 days absence), the pattern of recaptures suggests that many of the fish had been migrating to the north.

To some extent, the recapture of a relatively large number of fish from the Moray Firth is likely to be associated with the large amount of seine-net fishing that goes on there. Commercial fishing off the Scottish east coast tends to be greater at the latitude of the Moray Firth than at the latitude of the Bell Rock and this can be expected to impose an apparent northerly trend on to the results. However, comparison of the May 1957 experiment with the November/December 1957 experiment (Fig.2) shows that the results cannot be entirely explained in this manner. During the first six months after liberation, returns from the May 1957 experiment came from all directions within a radius of 60 miles of the Bell Rock. During the first six months after the November/December 1957 liberation there were a considerable number of returns from the Moray Firth and further north. The difference between the two experiments is most striking and cannot be explained by the fact that there is a considerable amount of seine-net fishing in the Moray Firth. In fact there was considerable seine netting there for the six months after each date of liberation and if the movements of the fish had been the same on each occasion, at least some of the fish liberated in May 1957 should have been returned from the Moray Firth before January/February 1958.

Also, when at last there were Moray Firth returns of fish liberated in May 1957, no fish came back from corresponding distances to the south or west of the Bell Rock. This cannot be explained by lack of fishing there, or the fact that haddock do not frequent these regions, but suggests that movement in winter and spring was indeed towards the north.

The June 1956 experiment (Fig. 3) provided only 33 recaptures. These were distributed widely about the position of liberation and support the hypothesis that movements during summer and autumn are largely undirected.

Analysis of Results

The recapture data shown in Figures 1–3 give a strong impression that haddock off the east coast of Scotland tend to disperse at all times, but that in late winter and early spring there is a superimposed directional movement anti-clockwise around the Scottish mainland.

In the November/December 1957, and that part of the May 1957 experiment in which the fish appeared to be moving north, the majority of the fish were just approaching their third birthday. It is possible therefore that the northerly movement in winter and spring was associated with the coming maturity of most of these fish.

As a purely qualitative interpretation of the recapture data, this is probably sufficient but it remains to consider if it is possible to put these concepts on a quantitative basis. One way of doing this is by supposing that the movement

Figure 2. Distribution of 55 haddock returned out of 377 liberated in November/December 1957 off Bell Rock. Symbols as in Fig. 1.

Figure 3. Distribution of 33 haddock returned out of 240 liberated in June 1956 off Findon Ness. Symbols as in Fig. 1.

of each haddock can be expressed as the resultant of two components. First, any tendency for haddock to move in a particular direction is to be defined as a directional movement. This can be measured in miles/day. Secondly, since

it is unlikely that all haddock move in the same direction at the same time, there must also be a certain amount of undirected movement relative to one another and this will show itself by a certain amount of dispersion of the liberated fish.

Consider the purely undirected or random movements first. This can be done, quantitatively, by supposing that movement is made up of a series of short "steps". At any moment a fish can be supposed to move a certain distance in a straight line, in any possible direction. The net movement is then made up of the sum of a very large number of such "steps", each of which can be orientated with respect to the others in any possible direction with equal likelihood. For example, in Figure 4 is shown the locus of all possible positions that a fish might have been at, prior to its appearing at position A. Here the unit "step" is supposed to be of length ε, i. e., fish at point A must have come from some position on the circumference of a circle with centre A and radius ε. Similarly, after its arrival at A, its next "step" will take it back to some position on the circumference of the same circle. If a large number of fish are liberated simultaneously and proceed to move in this sort of manner, and independently of one another, a gradual dispersion of individuals will occur. The overall displacement of the group will be zero, however, since for every fish found x miles in one direction from the origin, one can expect to find another also with displacement x miles, but situated in exactly the opposite direction.

The mathematics of a process such as this have, rather conveniently, been developed in some detail in connexion with physical theories of diffusion and the conduction of heat. A useful description of the theory is given by Domb (1946) and Skellam (1951). Wilkinson (1952) uses it to analyse bird movements and it is also used by Beverton and Holt (1957) as the basis for some of their theoretical work on fish movement. In order to make the analysis applicable to the tagging results described here, it has been supposed that, in addition to random movements, there is a superimposed directional component of the movement such that the centre of density of the whole fish group actually moves with some velocity V. The presence in these experiments of a coastline near the point of liberation does not unduly complicate the analysis, provided it is supposed that the direction of movement is parallel to the coast and that the fish are tagged close to the coast. It is thought that these assumptions are reasonable.

The theory can be further simplified if the distribution of fishing effort in the recapture area is assumed to be uniform. As in fact, there is a tendency for the fishing effort to increase to the north of the liberation positions, the adoption of this assumption leads to over-estimates of the northerly component of movement.

Details of the theory are given below where formulae are derived for estimating V, the directional component of the fishes' velocity, and a^2, which is the mean square dispersion (Skellam, 1951) or simply the dispersion coefficient. These are:—

$$V = \frac{\Sigma r \cos\theta}{\Sigma t}$$

and

$$a^2 = \frac{1}{n}\left[\Sigma\frac{r^2}{t} - \frac{(\Sigma r\cos\theta)^2}{\Sigma t}\right] \quad \ldots\ldots\ldots\ldots\ldots\ldots (4)$$

where, for each fish returned:

r = apparent "straight line" distance travelled,

t = number of days free,

θ = direction of travel measured from the axis of the coastline (see Fig. 5),

n = number of returns.

An example of the method of computation is given in Table 1 for 5 purely hypothetical returns.

Table 1

Showing the recapture details for 5 fish (hypothetical example)

Direction of travel (θ)	$\cos\theta$	Distance travelled (r) miles	Days absence (t)	$r\cos\theta$	$\frac{r^2}{t}$
–	–	0	100	0	0
40°	·766	50	200	38·3	12·50
50°	·643	5	75	3·2	0·33
90°	0	10	50	0	2·00
150°	−·866	20	100	−17·3	4·00
Total			525	24·2	18·83

The columns in this table give the recapture details for each fish in terms of direction θ, distance r, and days absence t, and also the first steps in the derivation of the movement parameters. From the "total" figures in the bottom row, we get the following identities:—

$$\Sigma t = 525$$
$$\Sigma r\cos\theta = 24{\cdot}2$$
$$\Sigma \frac{r^2}{t} = 18{\cdot}83$$
$$n = 5 \text{ (the total number of recaptures)}$$

Using these values, the formula (4) can be applied, giving

$$V = \frac{24{\cdot}2}{525} = 0{\cdot}046 \text{ miles/day}$$

$$\text{and } a^2 = \frac{1}{5}\left[18{\cdot}83 - \frac{(24{\cdot}2)^2}{525}\right] = 3{\cdot}54 \text{ miles}^2\text{/day}$$

One concludes that the movements of the fish returned are consistent with a mean square rate of dispersion of 3·54 miles^2/day, with a superimposed directional velocity of 0·046 miles per day along the coast. The actual direction of this movement depends on whether V is positive, as in this instance, or negative.

The coefficient of dispersion a^2 is in units of miles^2/day. This is because it is dependent on both the swimming speed of the fish and also on the average distance travelled between each change of direction (BEVERTON and HOLT, 1957). A given rate of dispersion could be the result of a group of fish swimming rapidly with frequent changes of direction, or slowly with less frequent turns. It follows therefore that it is not possible, from the distribution of returns alone, to discriminate between these alternatives. Instead one obtains a

measure of a parameter, (a^2) that is dependent both on swimming speed and on the mean distance travelled without change of direction.

Estimates of V and a^2 for each experiment have been determined and are shown in Table 2.

Table 2

Showing the estimated values of V and a^2 for different haddock tagging experiments

Date	Year-class	Directional component of movement (V) miles/day	Dispersion coefficient (a^2) miles²/day
June 1956	1954	−0·076	20·5
May 1957 to 18. November ...	1955	0·024	2·2
After 18. November	1955	0·17	35·6
Nov./Dec. 1957	1955	0·82	118

Directional movements

Estimates of the directional component of the movements are given in the third column of Table 2.

During the summer and autumn months following both the June 1956 and the May 1957 liberations, the degree of directed movement appears to be very small. In 1956 it averaged — 0·076 miles per day and in 1957 it averaged 0·024 miles per day. The negative sign before the 1956 value indicates that the mean displacement was to the south. In 1957 it was to the north. Taken singly, these values are very small and together they practically cancel out each other. The implication is that during the summer and autumn months, two year-old haddock off the Scottish east coast do not migrate in any one direction.

After a date about the middle of November (arbitrarily taken as 18. November) returns from the May 1957 experiment began to come in from positions in the Moray Firth and further north. This was particularly noticeable in January and February after about 250 days absence. The mean northerly displacement of all fish returned after 18. November was 0·17 miles per day. It seems reasonable to suppose that these fish had been moving north at no more than 0·024 miles per day prior to that date, so that the mean value of 0·17 miles per day would be an underestimate of their northerly drift after 18. November. The calculation depends on just how long they spent moving at 0·024 miles per day which is unknown. If six months is assumed, then their northerly shift subsequent to 18. November must have been about 0·4 miles per day which is quite considerable.

It is interesting to compare this value with that calculated from the returns of fish that were actually liberated in November 1957. The mean value calculated from these was 0·82 miles per day and is even higher. Subsequent considerations, however, suggest that this may be a slight overestimate of the general northerly trend and that 0·68 may be a more realistic value and, incidentally, one that agrees quite well with the estimate of 0·4 miles per day from the May 1957 experiment.

The conclusions to be drawn from these estimates of the coefficient V seem to be that

(a) during the summer and autumn months there was no migratory tendency amongst the tagged fish;

(b) during the winter and spring there was a real northerly movement of about 0·4 – 0·7 miles per day. Furthermore, in view of the unequal distribution of fishing effort, this is likely to be an overestimate of the northerly movement.

Rate of dispersion

Estimates of the dispersion coefficient a^2 are given in the last column of Table 2. These are very variable, and more difficult to interpret.

Some indication of the cause of this variation comes to light if individual values of a^2 are determined for each recapture. This can be done in a way that is described in the appendix and a frequency distribution of the values of a^2 can then be prepared. For the November/December 1957 experiment, for example, this distribution is given in Table 3.

Table 3

Frequency distribution of the values of a^2 calculated from the 34 returns of the 1955 brood

a^2	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55
Number	2	1	4	4	5	1	1	2	1	1	2

plus $\frac{1}{96}$ $\frac{1}{123}$ $\frac{1}{168}$ $\frac{1}{170}$ $\frac{1}{178}$ $\frac{1}{180}$ $\frac{1}{222}$ $\frac{1}{335}$ $\frac{1}{686}$ $\frac{1}{1280}$

Theoretical considerations, given below, suggest that, ideally, the frequency distribution of the values of a^2 should be exponential. The distribution shown in Table 3 is far from exponential and also, due to the existence of a number of extremely high values, the mean (which is equal to 118) is hardly representative of the distribution as a whole.

The presence of this "tail" of very high values of a^2 is due to fish that had travelled round to the north and west coasts of Scotland in comparatively short periods of time. For example, the value of $a^2 = 1280$ was calculated from a fish that was recaptured off Shetland, after travelling 244 miles in only 36 days. This is a considerable movement and it is possible that the whole journey was undertaken in the one direction with comparatively little undirected or random movement. The likelihood of this happening, if the fish was moving at random is very small. In Table 3 there are at least eight unlikely values of a^2 and these suggest that another interpretation altogether should be placed on these results. Instead of supposing that the movements of the fish can be expressed simply by two components (a) a northerly shift and (b) some degree of undirected movement, it is necessary to suppose that in addition, the degree of northerly shift can be extremely variable. If this is true, it explains why the distribution in Table 3 departs from exponential due to the presence of a "tail" of high values of a^2. It is worth remarking that if the fish that gave rise to the eight highest values in Table 3 are ignored, the remaining 26 fish give a value of $V = 0{\cdot}68$ miles/day and a value of $a^2 = 29$ miles^2 per day. This represents a substantial reduction in a^2, but it is probably still an overestimate. The best conclusion to be drawn from these considerations is that where there is any substantial directional movement, estimates of a^2 by the method adopted here are likely to be overestimated by an amount that depends on any variation that may occur in the directional movement of individual fish. It seems advisable

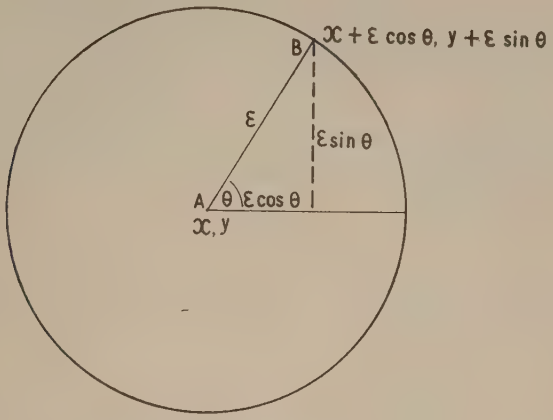

Figure 4. Locus of all possible positions of a fish at an instant of time previous to its being at point A.

therefore to estimate a^2 only from those experiments in which there is no evidence of directional movement. In these experiments, this means accepting only the estimates of a^2 obtained from the June 1956 experiment (20·5 miles^2 per day) and from the first part of the May 1957 experiment (2·2 miles^2 per day). Even these differ considerably from each other but in the absence of any further information must be accepted as the best estimates available from the data. For comparison, the value of a^2 obtained for plaice by BEVERTON and HOLT (1957) was 1–2 miles^2 per day.

Theoretical Section

Referring to Figure 4 it will be supposed that, during a short interval of time w, each fish moves along a straight path of length ε. It then follows that, if at some time $t + w$, a fish is situated at a position with co-ordinates x, y (point A in Fig. 4), it must at the previous instant t have been situated somewhere on the circumference of the circle with centre A and radius ε. At any particular point on this circle, such as B, the co-ordinates of its position are $x + \varepsilon \cos \theta$, $y + \varepsilon \sin \theta$. The probability that it moves in the particular direction from B to A is constant, and equal to $d\theta/2\pi$.

This, incidentally, is the basis of the mathematical theories of diffusion and heat conduction, and the details can be found in text-books on the calculus. A useful outline of the theory is given by SKELLAM (1951) and it is also used by BEVERTON and HOLT (1957). The arguments below will be developed as an extension to the approach outlined by SKELLAM.

In addition to random movements, it will be necessary to take account of a directional velocity V, and a mortality coefficient Z. Let us arrange matters so that the directional movement is along the y axis of our co-ordinate system. Then, a fish at point A (Fig. 4), at time $t + w$, must previously at time t have been somewhere on a circle of radius ε and centre x, $y - Vw$. The point B would then have had co-ordinates $x + \varepsilon \cos \theta$, $y - Vw + \varepsilon \sin \theta$.

Let $N(x, y, t)$ be the density of fish at the point, x, y at time t, so that the actual number in small area $dx\,dy$ can be denoted by

$$N(x, y, t)\,dx\,dy$$

Then, in the absence of any deaths, the number at point A at time $(t + w)$ will be the sum of all those moving in from the circle of radius ε and centre $x, y - Vw$, i. e.,

$$N(x, y, t + w) = \frac{1}{2\pi} \int_0^{2\pi} N \left\{ x + \varepsilon \cos \theta, y - Vw + \varepsilon \sin \theta, t \right\} d\theta$$

If, during the interval w, a proportion of those alive equal to Zw die, then we have

$$N(x, y, t + w) = \frac{(1 - Zw)}{2\pi} \int_0^{2\pi} N \left\{ x + \varepsilon \cos \theta, y - Vw + \varepsilon \sin \theta, t \right\} d\theta$$

Expanding by TAYLOR'S theorem, one obtains, in the limit, for small ε and w, the relation,

$$\frac{dN}{dt} = \frac{a^2}{4} \nabla^2 N - V \frac{dN}{dt} - ZN \quad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

The solution to this equation depends on the boundary conditions. In order to introduce a coastline, it is convenient to suppose that this passes through the point of liberation and is co-incident with the y-axis. The boundary conditions are then:—

$$\frac{dN}{dx} = 0 \text{ when } x = 0$$

$N = T$ when $t = 0$, $x = 0$ and $y = 0$,
$N = 0$ when $t = 0$ for all other values of x and y, where T is the number of fish tagged.
The solution to (1) is then

$$N = \frac{2T}{a^2 t \pi} \exp\left[- \frac{1}{a^2 t} \left(x^2 + (y - Vt)^2 \right) - Zt \right] \ldots\ldots\ldots (2)$$

where x extends from 0 to ∞ and y extends from $-\infty$ to $+\infty$.

In practice, it is convenient to refer to the position of recapture of each fish in terms of a compass bearing and its distance from the point of liberation. If (2) is therefore transformed to polar co-ordinates, we obtain

$$N(r, \theta, t) = \frac{2T}{a^2 t \pi} \exp\left[- \frac{1}{a^2 t} \left(r^2 - 2 r Vt \cos \theta + V^2 t^2 \right) - Zt \right] \quad (3)$$

where $N(r, \theta, t)$ is the density per unit area of fish at a distance r and an angle θ from the point of liberation, after a time t.

Since it has been assumed all along that the rate of fishing and hence mortality is everywhere the same, it follows that the distribution function (3) can also be used to represent the distribution of fish recaptured after t days absence.

The parameters that have to be estimated are V, the rate of "drift" along the coastline, and a^2, which may be called the mean square dispersion coefficient (SKELLAM, 1951) or more simply the dispersion coefficient.

Applying the maximum likelihood method of estimation to equation (3) leads to the following estimates of V and a^2

$$\left.\begin{aligned} V &= \frac{\Sigma r \cos\theta}{\Sigma t} \\ a^2 &= \frac{1}{n}\left(\Sigma\frac{r^2}{t} - \frac{(\Sigma r\cos\theta)^2}{\Sigma t}\right) \end{aligned}\right\} \quad \ldots\ldots\ldots\ldots\ldots (4)$$

It is to be noted that these are independent of the mortality coefficient Z.

Distribution of the quantity, R^2/t

Equation (3) can be made symmetrical by eliminating V. This can be done be making the transformation,

$$r\cos\theta - Vt = R\cos\varphi$$
$$\text{and } r\sin\theta = R\sin\varphi$$

This is equivalent to considering the distribution about a point $(0, Vt)$ which is the centre of density of the fish after time t.

$$N(R, \varphi, t) = \frac{2T}{a^2 t\,\pi}\exp\left[-\frac{R^2}{a^2 t} - Zt\right] \ldots\ldots\ldots\ldots (5)$$

Integration with respect to φ can be performed easily giving the density of fish at a distance R from the origin, irrespective of direction. If this is denoted by $N(R, t)$, we get

$$N(R, t) = \frac{2TR}{a^2 t}\exp\left[-\frac{R^2}{a^2 t} - Zt\right] \ldots\ldots\ldots\ldots (6)$$

Let us now evaluate R^2/t for each fish and denote it by x. The frequency distribution of x can be obtained by substitution in (6) and becomes:

$$f(x, t) = \frac{T}{a^2}\exp\left[-\frac{x}{a^2} - Zt\right] \ldots\ldots\ldots\ldots (7)$$

Now, $T\exp[-Zt]$ is the total number of fish alive at age t. If this is denoted by $N(t)$ the probability of x falling in the range x, $x + dx$ can be written $\frac{1}{N(t)} f(x, t) = \frac{1}{a^2} e - \frac{x^2}{a^2}\,dx$, which is independent of t.

If, then, the numbers of fish having values of x in unit intervals are determined, these can be expected to conform to an exponential frequency distribution. Also the natural logarithms of these numbers should lie on a straight line with a slope equal to $-1/a^2$.

Furthermore, from its derivation, it is apparent that each value of "x" is an estimate of a^2 calculated for an individual fish. The distribution of "x" is therefore the distribution of individual values of a^2.

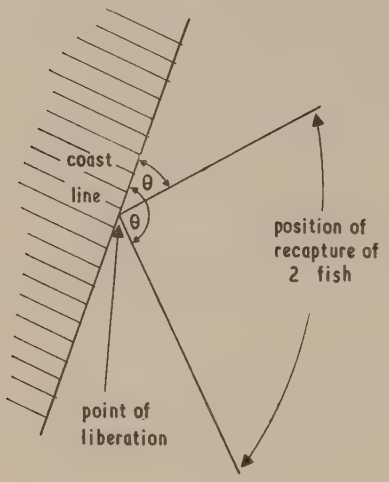

Figure 5.

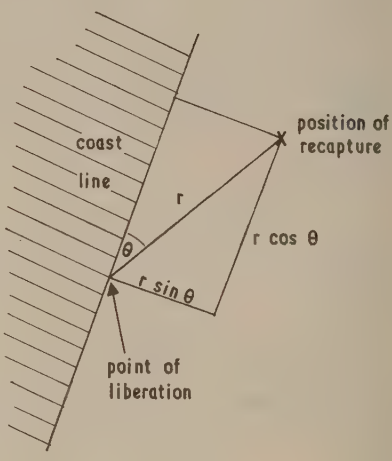

Figure 6.

Figure 5. Showing the method of measuring the angles θ between the coastline and the direction of travel of each fish.
Figure 6. Showing the resolution of a distance travelled r into two components, $r \cos \theta$ along the coast and $r \sin \theta$ at right angles to the coast.

Appendix

Below is given an example, showing the method of calculating individual values of a^2 for each of five fish.

Table 4

Showing the method of calculating a value of a^2 for each fish individually, when $V = 0{\cdot}82$ miles/day

θ	r	t	$\cos\theta$	$\sin\theta$	$r\cos\theta$	Vt	$A = r\cos\theta - Vt$	$B = r\sin\theta$	$\frac{A^2+B^2}{t} = a^2$
−5	2	11	0·996	−0·087	2·0	9	−7	−0·2	4
25	3	13	0·906	0.423	2·7	11	−8·3	1·3	5
68	0·5	26	0·375	0·927	0·2	21	−20·8	0·5	17
−7	244	36	0·992	−0·122	242	30	212	−29·8	1273*
−8	221	76	0·990	−0·139	219	62	157	−30·7	337*

* These values differ slightly from those quoted in Table 3, due to rounding errors in Table 4.

The first three columns of Table 4 give the basic recapture data: direction, distance travelled, and days absence. In Figure 6, it is shown how the distance travelled r can be resolved into two components, $r \cos \theta$ along the coast and $r \sin \theta$ at right angles to the coast. These values are shown for each fish in Table 4. From the complete data it has been estimated that each fish is moving north with an average velocity of 0·82 miles per day so that after t days absence

each will have moved a distance of 0·82 t miles. This is given for each fish in the column headed Vt. Column A measures $r \cos \theta - Vt$ which would have been the northerly displacement of each fish if there had been no directional movement. The sum of squares of columns A and B (i. e., $A^2 + B^2$) is therefore a measure of what r^2 would have been in the absence of northerly movement. The final column is therefore an estimate of r^2/t in the absence of northerly movement, i. e., a measure of dispersion a^2.

Table 4 gives the results for five fish. When the results for all fish are worked out in this way it is possible to draw up a frequency distribution of the individual estimates of a^2. This is shown in Table 3 above.

Acknowledgements

The author wishes to express his thanks to members of the Marine Laboratory staff, Aberdeen, for their critical reading of the manuscript and their assistance in tagging fish and also to J. A. GULLAND of the Fisheries Laboratory, Lowestoft, for his helpful comments.

Summary

1. Haddock were tagged off the Scottish east coast in June 1956, May 1957, and November/December 1957.

2. The majority of fish recaptured were two, or just three years old and, in the case or recaptures during spring, could conceivably have been about to spawn for the first time. Recaptures of older fish were poor, simply because fewer had been tagged, and so the method of analysis and the conclusions reached in this paper apply only to the 2–3 year-old fish.

3. A preliminary inspection of the recaptures (see Figs. 1–3) led to the following conclusions:—

(a) during the summer and autumn, haddock off the Scottish east coast did not show any migratory tendency, but merely dispersed from the positions of liberation in a "random" manner;

(b) during winter and spring, a real trend, anticlockwise round the Scottish mainland, was discernible.

4. Further analysis of these data was attempted by making the assumption that the movement of each fish at any instant could be divided into two components:—

(a) a directional component acting in the direction of the coastline, and

(b) an undirected, or random component, with respect to other individuals leading to dispersion.

5. Estimates of the directional component confirmed that this was negligible during the summer and autumn months. During the winter and spring, there was a real anticlockwise trend averaging 0·4 – 0·7 miles per day. Due to some irregularity in the distribution of fishing effort, it is probable that this is an overestimate. Further analysis revealed that in all probability there was a considerable individual variation in the directional rates of movement. Those for some fish, which were returned from the north and west coasts after comparatively short periods of absence, were particularly large.

6. The effect of such variations was to overestimate values of the coefficient

of random movement. Therefore only those experiments in which no directional movement was detectable were used for estimating the degree of undirected movement. In this way, estimates of the dispersion coefficient ranging from 2–20 miles^2 per day were obtained.

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Fecundities of Winter-Spring and Summer-Autumn Herring Spawners

By

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Introduction

The possibility that fecundity differences might be used for separating different stocks of herring was first suggested by FARRAN (1938) who showed that on the Irish coast spring spawning and autumn spawning herring of the same length had different fecundities. HICKLING (1940), working on the fecundity of the herring of the southern North Sea, obtained results for that stock which were similar to those of spring spawners on the Irish coast. He considered that the fecundity of herring was related to the spawning season, summer spawners producing the largest number of eggs and winter or spring spawners producing the smallest number. More recently KÄNDLER and DUTT (1958) suggested that in the Baltic the fecundity of herring was related to the environment in the area in which spawning took place. They found that the spring spawners of the western Baltic produced more eggs than the spring spawners in the central Baltic and also that Baltic herring have higher fecundity than Dogger Bank autumn spawners.

Fecundity investigations were started at the Marine Laboratory, Aberdeen, in 1957, to study the fecundity of different groups of herring spawning in the North Sea and adjacent areas in order to help in establishing the identity of these groups and their relationships.

In this paper the fecundities of the summer-autumn spawners, spawning in the north-western North Sea, off the Scottish east coast in August-September, and in the Southern Bight of the North Sea and eastern part of the English Channel in November–December, are compared and similarly the fecundities of the spring spawners of the Norwegian and Clyde fisheries.

I wish to thank my colleagues in England and Norway for sending samples of East Anglian and Norwegian herring for this investigation. I am also indebted to Mr. W. HALL for his help with the mathematical equations, and to Mr. B. B. PARRISH for helpful advice and suggestions.

Methods

The material used in this paper was collected between February 1957 and March 1958. The collections were made from Clyde spring spawners in February-March 1957 and 1958, Buchan autumn spawners in July–August 1957, East Anglian autumn spawners in October and December 1957, and Norwegian spring spawners in February 1958. From each fish the length, total weight, and weight of ovary were recorded; otoliths and scales were taken for age determination.

The methods adopted for the treatment of the ovaries were those used by SIMPSON (1951). The ovaries were placed in jars and preserved in a modified version of GILSON's fluid. Vigorous shaking of the jars helped to loosen the ovarian tissue and ensure rapid penetration of the preserving fluid. After a period of at least 48 hours the jars were then shaken vigorously again to liberate eggs from the ovarian tissue. The eggs were then washed thoroughly and after filtering off the excess water they were spread out on blotting paper and left to dry in air. The estimations of the fecundity were obtained by weighing the total number of eggs and then counting weighed random samples of about 500 eggs and raising by the ratio total weight/weight of sample.

Results

The results are presented in the following manner: firstly, a comparison is made of the fecundities of the northern and southern North Sea summer and autumn spawners, followed by a comparison of the fecundities of the Norwegian and Clyde spring spawners. Finally, the sizes of eggs of the four groups of spawners are compared.

Northern North Sea summer-autumn and Southern Bight autumn spawners

In Figure 1 the relationships obtained between fecundity and length are shown for the spawners from both regions and can be expressed by the following equations:—

$$\text{Northern North Sea spawners } F = 0{\cdot}1980\, L^{3.8417}$$
$$\text{Southern Bight spawners } F = 0{\cdot}02185\, L^{4.3290}$$

where F and L represent fecundity and length.

It is seen that the northern spawners have a significantly higher level of egg production than the southern spawners. There is little or no overlapping between them. The relationship between fecundity and length shown for the northern spawners is very similar to the results obtained by FARRAN (1938) for the Irish coast autumn spawners and the Southern Bight data are similar to those produced by HICKLING (1940) for the same group in 1933.

The relationships between fecundity and weight for northern North Sea and Southern Bight spawners are given in Figure 2. It is seen that the fecundities of the two groups are distinct at any given weight. The relationship between fecundity and weight appears to be linear and the lines giving the best fit for the fecundity weight relationships are expressed by the following equations:—

$$\text{Northern North Sea spawners } F = 481{\cdot}03W - 19{,}304$$
$$\text{Southern Bight spawners } F = 277{\cdot}77W - 12{,}768$$

where F and W refer to fecundity and weight.

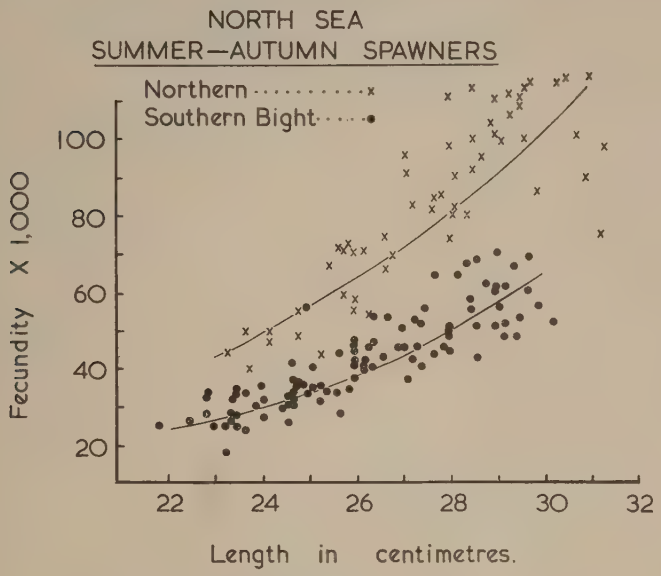

Figure 1. The relationship between fecundity and length.
Each dot or cross refers to one fish.

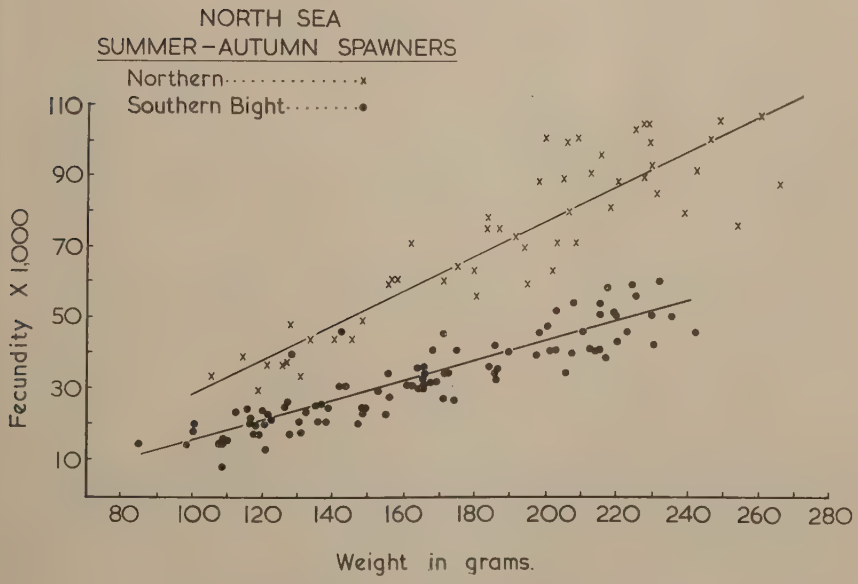

Figure 2. The relationship between fecundity and weight.
Each dot or cross refers to one fish.

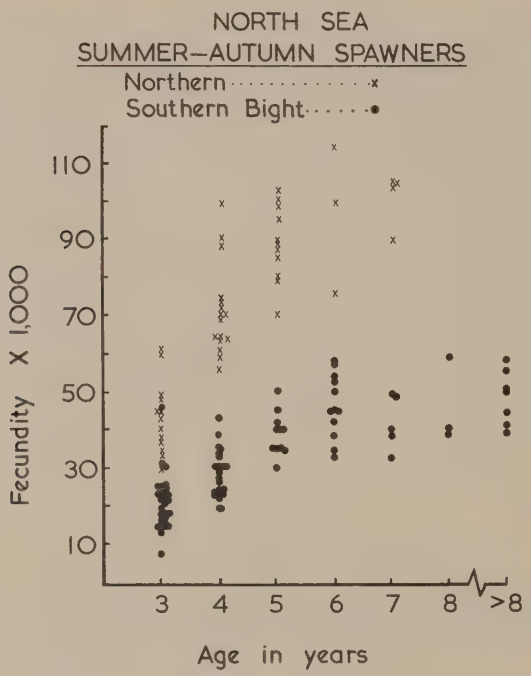

Figure 3. The relationship between fecundity and age. Each dot or cross refers to one fish.

In Figure 3 the relationships between fecundity and age irrespective of length and weight are shown. The differences between the fecundities of the northern North Sea and Southern Bight spawners appear to be even more distinct on an age than on length or weight bases. There is a very small overlap amongst the three year-old recruit spawners. The smallest three year-old northern spawners have a similar fecundity to the largest three year-old southern spawners.

Norwegian and Clyde spring spawners

The relationships between fecundity and length for the Norwegian and Clyde spring spawners are shown in Figure 4 and are expressed by the following equations:—

Norwegian spring spawners $F = 0{\cdot}03269\, L^{4.0877}$

Clyde spring spawners $F = 0{\cdot}0823\, L^{3.9131}$

where F and L represent fecundity and length.

There is only a short range of length over which these stocks are comparable, i. e., 28–33 cm, but it would appear that over that range the level of egg production of the Norwegian herring is lower. The relationship shown for the Clyde herring is fairly similar to that obtained by Farran (1938) for spring spawners on the Irish coast, and also for the East Anglian herring in the present investigation.

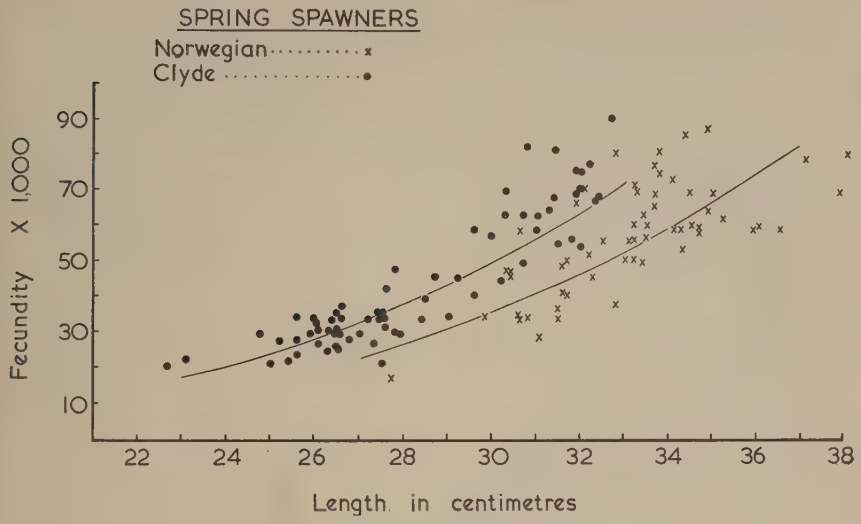

Figure 4. The relationship between fecundity and length.
Each dot or cross refers to one fish.

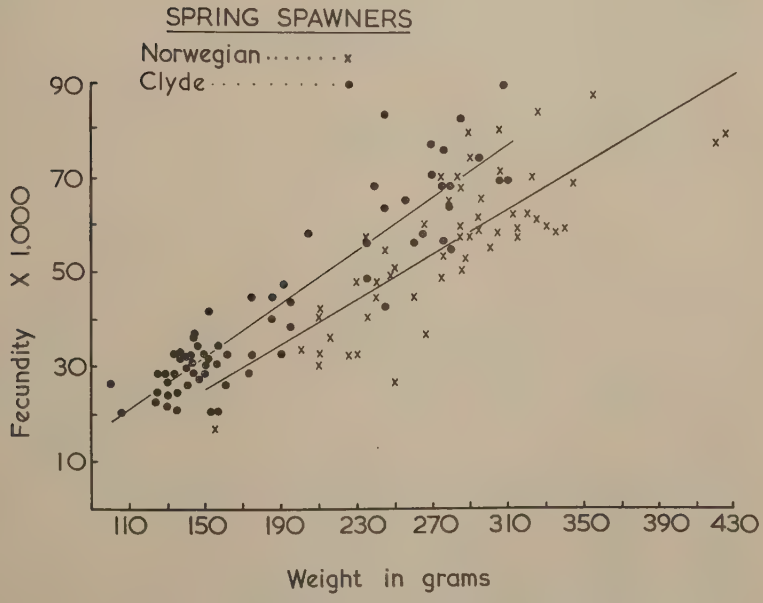

Figure 5. The relationship between fecundity and weight.
Each dot or cross refers to one fish.

The relationships between fecundity and weight for both groups of spring spawners are given in Figure 5 and are expressed by the following equations:—

Norwegian spring spawners $F = 240{\cdot}27\ W - 10{,}551$

Clyde spring spawners $F = 283{\cdot}04\ W - 9{,}937$

where F and W represent fecundity and weight.

In both groups it was found that there was a considerable variation in fecundity of fish of the same weight.

There are not sufficient comparable data on age of Norwegian and Clyde spawners to make a comparison of the relationships between fecundity and age.

Fecundity and egg size

The fecundity of herring appears to be related to the size of egg as well as length and weight.

The diameters of the eggs at spawning for the four groups of spawners under review are given in the below.

Norwegian spring spawners	1·5–1·7 mm
Clyde spring spawners	1·4–1·5 mm
Southern Bight autumn spawners	1·4–1·5 mm
Northern North Sea, Scottish summer-autumn spawners	1·1–1·2 mm

The Clyde and Southern Bight herring have the same size of eggs and similar fecundities. The size of egg of the northern, Scottish herring is about 25% smaller than Clyde or Southern Bight herring but they have a much higher fecundity. The Norwegian herring have a larger egg than the Clyde spring spawners and a lower level of fecundity over comparable ranges of length and weight.

Therefore the smaller the egg produced the greater the fecundity and vice versa. It would appear that the factors which determine the numbers of eggs to be produced also determine the size of egg.

Discussion

The recent changes and developments in the North Sea herring fisheries, and especially the decline in the East Anglian fishery, has increased the urgency for fresh data which might help in establishing the identity of the stocks of herring in the North Sea and the extent to which they are exploited by various fisheries at different periods of their annual life cycle. The East Anglian fishery in October and November is dependent mainly on herring which are in an advanced stage of maturity (Stages IV and V). These herring spawn on banks at the entrance to and in the eastern part of the English Channel in November and December and have been termed the Downs herring; and those spawning on the Dogger and further to the north, the Bank herring (CUSHING, 1955; KREFFT, SCHUBERT, and SAHRHAGE, 1955). Apart from a difference in spawning time and spawning place, the degree of separation between the Bank and Downs herring is not clearly understood, but there are some data which indicate that during some periods of the year, especially the spring and early summer, the adults of both groups are to be found feeding together in the

northern North Sea. It is believed that some of the progeny of both groups are carried by drift currents to the same nursery grounds along the coast of Germany and Denmark where they develop together.

The results from the present investigations have shown that there is a significant difference between the fecundities of the herring which spawn off the Scottish east coast in August–September and those which spawn in the Southern Bight and English Channel in November–December. The northern, Scottish spawners have a much higher fecundity than the Southern Bight spawners. There appears to be little or no overlap in fecundity between them.

At this stage it is necessary to bridge the gap between these two distant spawning groups. Data are required, therefore, on the fecundity of other autumn spawning groups in the North Sea, and particularly of those herring which spawn on the Dogger Bank. KÄNDLER and DUTT (1958), for example, in their paper "Fecundity of Baltic herring" give some data for 40 Dogger Bank spawners which suggest that the smaller and younger Dogger spawners have fecundities which are similar to those obtained for the Southern Bight spawners, while the larger and older herring have fecundities which are similar to the northern or Scottish herring.

In the interpretation of differences in fecundity between spawners in two different areas it is important to know whether the differences obtained are due to genetical or environmental factors. If the differences between the fecundities of the northern North Sea and Southern Bight spawners shown here prove to be genetical, then they will provide useful evidence that these two groups of spawners are separate stocks. Unfortunately the extent of our present knowledge in this field is insufficient to provide a definite answer to this question. On the one hand, further investigation of the fecundity of the Dogger Bank spawners may help to suggest the type of factor which controls the number of eggs produced by herring. Another approach to this problem would be to conduct some experimental work with herring in tanks. It has been suggested (SIMPSON, 1951) that in some fish the number of eggs to be produced for each spawning is determined very soon after the previous spawning has taken place. Some indication of how early the fecundity is determined might be obtained by attempting to estimate the number of herring eggs during early stages of maturity and comparing these estimates with those obtained at more advanced stages of maturity.

Summary

1. In 1957 investigations were started at the Marine Laboratory, Aberdeen, to study the fecundity of different groups of herring spawning in the North Sea and adjacent areas, in order to help in establishing the identity of these groups and their relationships.

2. In this paper the fecundities of the summer-autumn spawners, spawning in the north-western North Sea, off the Scottish east coast in August–September, and in the Southern Bight of the North Sea and eastern part of the English Channel in November–December, are compared.

3. A comparison is also made between the fecundities of Norwegian and Clyde spring spawners.

4. On a length, weight, or age basis the fecundities of the northern North Sea summer-autumn spawners are significantly higher than those of the Southern

Bight autumn spawners. There is little or no overlap between the fecundities of the two groups.

5. Over comparable ranges of length and weight the fecundities of Norwegian spring spawners are lower than those of Clyde spring spawners.

6. In the groups under review fecundity is inversely related to the size of egg. The northern summer-autumn spawners have a relatively small egg and a high fecundity. Norwegian spawners have a relatively large egg and a low fecundity.

7. The extent of our knowledge at present is insufficient to state whether the differences in fecundity are due to genetical or environmental factors.

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Otolith Types amongst Summer-Autumn Spawning Herring in the Northern North Sea

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Introduction

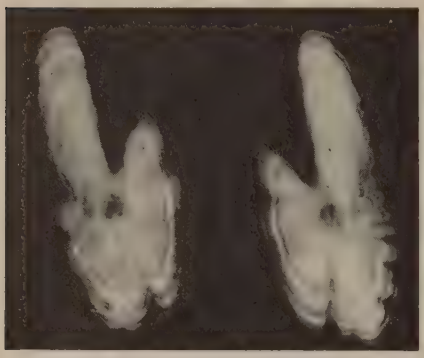
In recent years special attention has been paid by a number of herring workers to features of the otoliths of herring some of which fall into the category of "individual" racial characters (Einarsson, 1951; Parrish, *et al.*, 1956, 1957, 1958; Parrish and Sharman, 1958; and Postuma and Zijlstra, 1958).

In the earlier publication by the present authors, mention was made of differences between the forms of the first winter zones and the sizes of the first growth zones amongst members of the North Sea "summer-autumn" spawning herring population. Two main types of otolith were described: those with a "wide" first winter zone and a relatively small first growth zone, and those with a thin-sharp or "narrow" first winter zone and a relatively large first growth zone. Recent detailed analyses of otoliths from adolescent and adult herring localities have confirmed the presence of these types, which are illustrated in Figure 1. They have indicated that their occurrence amongst the adolescent and adult members of the "summer-autumn" spawning herring population may provide some important pointers to the nursery areas from which herring on different spawning grounds are derived, and the extent of the changes in composition of the fish spawning in each region from year to year. This paper deals with results of the preliminary analysis of these otolith features and other "racial" characters amongst spawners on the Scottish east coast spawning grounds and amongst the adolescent nursery concentrations from different parts of the North Sea.

Collection of Data

Extent of sampling

In the analysis conducted so far, attention has been paid chiefly to the occurrence of these otolith types amongst herring in maturity stages VI and VII from the Scottish east coast autumn spawning grounds in the years 1953–1956,



7 year-old herring from Scottish east coast spawning grounds, "narrow" type.

7 year-old herring from Scottish east coast spawning grounds, "wide" type.

2 year-old pre-recruit from Bløden nursery grounds, "narrow" type.

2 year-old pre-recruit from Bløden nursery grounds, "wide" type.

Figure 1. Examples of "narrow" and "wide" zoned otolith types from north-western North Sea and Bløden nursery grounds.

and to adolescent pre-recruit herring from the principal north-western North Sea nursery grounds in the upper reaches of the Moray Firth and the Firth of Forth. In addition, a small number of samples of adolescent herring from the Bløden nursery area and adult spawners from the East Anglian and Sandettié fisheries have been kindly supplied by the Danish and English laboratories.

All otoliths from these samples have been photographed and the identification of otolith types and measurements of the growth zones have been made from the photographic prints. A library of these prints is kept at the Marine Laboratory, Aberdeen.

Age, length, sex, and other "racial" data have also been recorded for all samples examined.

Photographic method

The technique of mounting and photography of otoliths differed in two ways from the method described by PARRISH and SHARMAN, 1958.

Mounting otoliths. A colourless transparent plastic resin (102) "Autoplax" manufactured by Automobile Plastics Co. Ltd., Barnet, England, was found to be more suitable than Canada balsam for mounting otoliths. The resin has similar physical and optical properties to Canada balsam with the advantage of a quicker drying time. The otolith is dried and mounted, without clearing, directly into the resin.

Photography. An improvement in lighting the otolith was made by using a Langham electronic flash ring illuminator instead of the earlier lighting arrangement. This provided a more even illumination. The ring illuminator is $2\frac{1}{2}''$ in diameter and fits round the camera extension tube.

Results

Distribution of otolith types amongst Scottish spawners

The occurrence of the two otolith types with "narrow" and "wide" first winter zones respectively amongst the age-groups present in the Scottish east coast spawning concentrations in each of the years 1953–1956 is given in Table 1. Included in this table are the otoliths which could not be categorized under either of these major types, due to a variety of reasons including broken and decalcified otoliths, and doubtful types. The last of these causes contributed between 2–8% of all the otoliths examined.

The most important features of these data are as follows:—

(1) In all years sampled, the 3 year-old recruit spawners consisted almost exclusively, if not exclusively, of the "narrow" zoned otolith type. No "wide" zoned otoliths were identified amongst the 3 year-olds in any of the years.

(2) Members of the "wide" zoned type appeared in varying proportions in all age-groups older than 3. For most of the year-classes sampled at successive ages, the proportion of this type increased at least up to age 6.

(3) The proportions of the two otolith types differed significantly between year-classes. The 1951 and 1952 year-classes contained a relatively low proportion of the "wide" zoned type in the years in which they were sampled as 4 and

Table 1

Percentage distribution of otolith types in spawning concentrations in the years 1953–1956

(N="Narrow" type; W="wide" type; U=unclassified)

Age	3			4			5			6			7			8–10			>10			Otoliths examined
Year / Type	N	W	U	N	W	U	N	W	U	N	W	U	N	W	U	N	W	U	N	W	U	
1953	93	0	7	60	31	9	67	23	10	47	43	10	47	44	9	55	37	8	59	35	6	456
1954	94	0	6	79	16	5	67	30	3	75	22	3	59	38	3	64	33	3	69	26	5	362
1955	96	0	4	82	5	13	67	20	13	38	45	17	58	27	15	52	42	6	62	25	13	923
1956	98	0	2	83	4	13	84	9	7	71	20	9	51	36	13	50	42	8	68	25	7	1901
Mean	96	–	4	76	14	10	71	21	8	58	33	9	54	36	10	55	39	6	65	28	7	

Table 2

Percentage distribution of otolith types amongst 2 year-old herring from Moray Firth and Firth of Forth nursery areas. 1952–1956

Year	Moray Firth				Firth of Forth			
	N	W	U	Otoliths examined	N	W	U	Otoliths examined
1952–53	96	0	4	268	–	–	–	–
1953–54	93	0	7	106	94	0	6	70
1954–55	100	0	0	84	89	8	3	93
1955–56	97	0	3	109	96	0	4	100

Table 3

Percentage distribution of otolith types amongst 2 year-old herring from Bløden nursery area in 1957

Sample	2 year–olds				3 year–olds			
	N	W	U	Otoliths examined	N	W	U	Otoliths examined
1	51	44	5	59	47	32	21	19
2	100	0	0	130	10	90	–	10
3	81	12	7	252	–	–	–	–
4	100	0	0	117	18	73	9	13
5	90	10	0	42	–	–	–	–

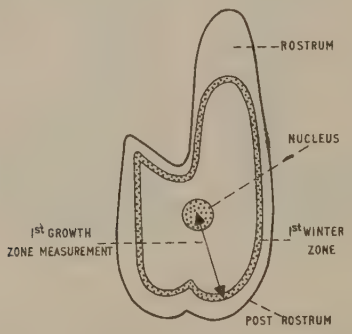


Figure 2. Illustration of otolith growth zone measurement.

5 year-olds and 4 year-olds respectively, while the year-classes 1948–1950 contained a much higher proportion of the "wide" zoned type between ages 4–7.

It is evident from these results that the spawners on the Scottish east coast grounds are heterogeneous with respect to otolith type. Can this information be used to trace their main sources of supply?

Otolith types of adolescent herring in North Sea nursery areas

In a search for the answer to this question, the otolith characters of herring from the main nursery areas in the North Sea and its vicinity are being studied. While only a preliminary survey has yet been conducted the results obtained reveal some important differences between the otolith types found on different

nursery grounds. Material has been examined from the winter fisheries in the main north-western North Sea nursery grounds in the upper regions of the Moray Firth and Firth of Forth for each of the years covered in the analysis of the spawners, and from the main southern North Sea Bløden nursery ground during the summer fishery in 1957.

The otolith types found amongst 2 year-old (one-ringed) herring on the northern grounds and of 2 and 3 year-olds (one and two-ringed) on the southern grounds are given in Tables 2 and 3 respectively.

All of the Moray Firth otoliths which could be classified were of the "narrow" type, and only 7 otoliths of the "wide" type were identified from the Firth of Forth material (263 otoliths). The compositions of the Bløden samples varied widely, but a substantial proportion of "wide" ringed type was present in some samples. Although the data from the southern North Sea are confined to only one year's sampling, these results suggest that the supply of the "wide" zoned otolith type amongst the adult spawners may well be from nursery areas to the south of the Scottish spawning grounds.

From these data it is not possible to specify the sources of supply of the "narrow" type spawners, since members of this type were present in both nursery areas. Further information on the identity of this type, however, is obtainable from the sizes of the first year growth zones. These were measured for all otoliths, the dimension measured being from the centre of the nucleus to the distal edge of the first winter zone, along an axis from the nucleus to the post-rostrum. This is shown in Figure 2.

Distribution of first growth zone measurements

The ranges and means of the first growth zone measurements made on the otoliths from each age-group of spawners in the years 1953–1956, and Moray Firth, Firth of Forth, and Bløden (1957) pre-recruits are given in Table 4. The frequency distributions of these measurements for the "wide" and "narrow" types amongst all age-groups of spawners in each year are given in Figure 3, and the frequency distributions of the measurements for the "narrow" type amongst the 3 year-old recruit spawners, the 2 year-old pre-recruits from the Moray Firth in the winter preceding each spawning season and the 2 year-old pre-recruits from the Bløden Ground, are given in Figure 4.

The most important features of these data are as follows:—

(1) The first growth zone measurements for "wide" otolith type spawners were smaller than for the "narrow" type spawners. In all years, the differences between the mean measurements for the two types were highly significant.

(2) For each otolith type amongst the spawners the distributions and means were similar between age-groups within a year-class and between year-classes.

(3) The distributions of zone measurements amongst the "narrow" type, Moray Firth pre-recruits and the "narrow" type spawners of all age-groups exhibit marked differences, and only a small degree of overlap. The difference between the means of the two groups is highly significant.

(4) The distributions for the "narrow" type recruit spawners and the pre-recruits from the Bløden area exhibit a much greater degree of overlap, and cover the same total range. For two of the five samples of otoliths from the Bløden area, the distributions of measurements agreed very closely with those of the recruit spawners.

Table 4

Ranges and means of first year growth zone measurements from photographs of "narrow" and "wide" otolith types amongs Scottish east coast spawners and Moray Firth, Firth of Forth, and Bløden adolescent herring (arbitrary units)

		Pre-recruits							
		Moray Firth[1])		Firth of Forth[1])		Bløden			
	Age	2						3	
Year	Type	Range	Mean	Range	Mean	Range	Mean	Range	Mean
1953	Narrow	14–25	19·9	–	–	–	–	18–30	25·1
	Wide	–	–	–	–	–	–	–	–
1954	Narrow	15–24	19·3	13–28	20·2	–	–	22–31	25·6
	Wide	–	–	–	–	–	–	–	–
1955	Narrow	16–27	20·6	16–27	20·2	–	–	16–31	25·0
	Wide	–	–	16–20	17·4	–	–	–	–
1956	Narrow	16–25	20·0	14–26	18·1	–	–	18–31	25·3
	Wide	–	–	–	–	–	–	–	–
1957	Narrow	–	–	–	–	18–31	24·0		
	Wide	–	–	–	–	15–23	19·5		

[1]) The Herring from the Moray Firth and Firth of Forth were sampled during the winter fishery preceding the spawning year; e.g., the data for 1953 refer to fish sampled in the winter of 1952–53.

The most striking result of this analysis is the difference between the distributions of measurements for the "narrow" type spawners and the pre-recruits from the neighbouring nursery areas in the Moray Firth and Firth of Forth. It appears that these nursery grounds supply only a very small proportion (if any) of the "narrow" type recruits to the Scottish spawning grounds. The data therefore suggest that recruitment is from elsewhere and possibly that, like the "wide" zoned type, these adults may be recruited principally from southern nursery areas.

Relation between otolith measurements and L_1's

The discrepancy shown between the otolith zone measurements for the Moray Firth pre-recruits and the recruit spawners of the same year-class is also revealed by L_1's calculated from scale measurements taken from the two groups. This is shown in Table 5, which gives the ranges and means of L_1's for the 3 year-old recruit spawners and the Moray Firth and Firth of Forth pre-recruits in the years 1953–1955.

A comparison of the otolith zone measurements and L_1's for the same samples of fish shows a high degree of correlation between them. Examples of this are illustrated in Figure 5 in which the relationships between L_1's and otolith measurements are shown for the "wide" and "narrow" zoned otolith types amongst the spawners in 1955, and the "narrow" type Moray Firth pre-recruits in the winter of 1952–1953. These results show a close linear relationship between the two sets of measurements for both otolith types.

Table 4 (continued)

Spawners													
Scottish east coast													
4		5		6		7		8–10		> 10		All ages	
Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
18–28	23·3	20–29	25·0	16–29	23·9	20–29	24·5	18–29	24·3	19–28	23·5	16–29	24·0
16–24	20·2	17–24	20·3	16–23	20·2	15–22	18·9	17–25	20·2	16–23	19·4	15–25	19·9
20–31	25·6	19–29	23·5	19–27	24·4	19–29	24·2	19–29	24·4	17–28	22·8	17–31	24·3
18–25	21·8	16–24	20·2	16–24	19·9	16–23	19·7	16–22	19·5	16–22	19·3	16–25	20·0
18–30	24·1	21–31	25·1	20–29	24·6	19–29	24·2	18–31	24·4	19–31	24·0	16–31	24·6
17–21	18·9	16–26	21·4	16–24	20·3	16–22	19·9	15–24	20·0	16–22	20·1	15–26	20·2
16–31	23·9	15–31	24·4	19–30	24·8	18–28	24·3	19–30	24·1	18–31	24·1	15–31	24·3
14–23	20·7	16–26	20·8	18–25	21·3	16–25	20·8	14–24	19·7	14–24	19·7	14–26	20·3

Discussion

The results presented above indicate that the study of these otolith features provides valuable information concerning the possible sources of supply of recruits to the Scottish spawning concentrations, and of the change in their composition with age. In each of the years investigated the spawners were composed of two otolith types, the relative proportions of which varied between year-classes and with age, at least up to age 6. Although the investigation of the pre-recruits from the southern North Sea nursery areas has been limited to a small number of samples from one year, the available evidence points to the "wide" zoned type being from southern nursery areas. It is significant in this respect that this type was the principal one found amongst samples of 3 year-old recruit spawners from the Sandettié region and pre-spawners from the East Anglian grounds in 1957. This is shown by the following breakdown of samples of 3 year-olds from these regions.

	Narrow %	Wide %	Unclassified %	Number of otoliths examined
East Anglia	8·1	80·6	11·3	110
Sandettié	0	87·0	13·0	134

The first growth zone measurements for the "wide" type otoliths in these samples coincided with those for this type in the Scottish spawning concentrations.

The analysis also indicates that the "narrow" zoned otolith type amongst the Scottish spawners in the years investigated may also have been derived chiefly from nursery areas to the south of the spawning area, and suggests that only a small part of the recruitment of this type came from the local nursery areas in the Moray Firth and Firth of Forth. As yet, the spawning areas supplied by

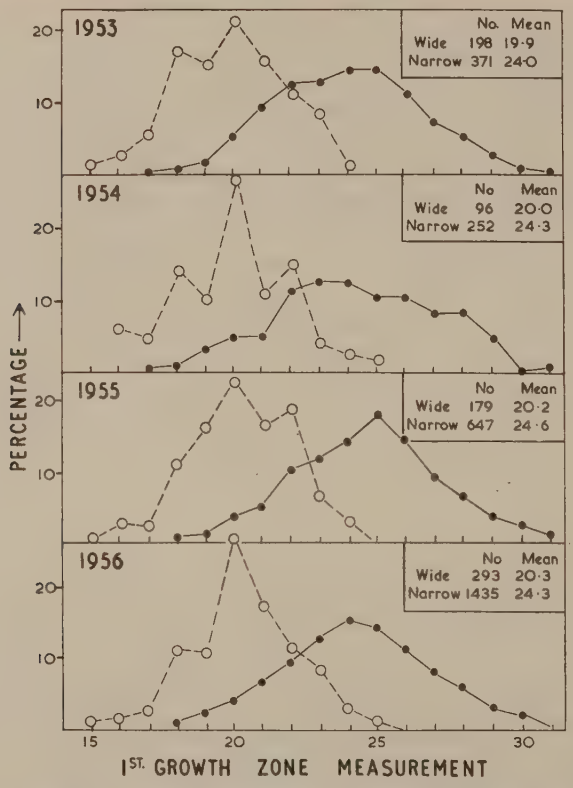


Figure 3. Frequency distributions of otolith zone measurements in "wide" (○--- ○) and "narrow" (●—— ●) types for Scottish east coast spawners. All age-groups combined. Frequencies unsmoothed.

the Moray Firth pre-recruits have not been identified, but it is of possible significance that a small number of measurements made on "narrow" type otoliths from the North Minch grounds off the Scottish west coast are in close agreement with those from the Moray Firth and Firth of Forth nursery areas.

With the data available at present it is not possible to assess the full biological significance of the differences between the two otolith types, or to gauge to what extent their occurrence together amongst the Scottish spawners is indicative of changes in the "racial" composition of the spawning concentrations from year to year. The close relationship between the otolith zone measurements and L_1's suggests that the difference between the growth zones of the "wide" and "narrow" types from the Bløden area is due to a slow or fast first year growth, resulting from either an early or late time of hatching or a difference in growth-rate. The difference between the size of the first winter zones in the two types is probably the result of metabolism and growth differences between herring inhabiting different areas. The two otolith features considered together

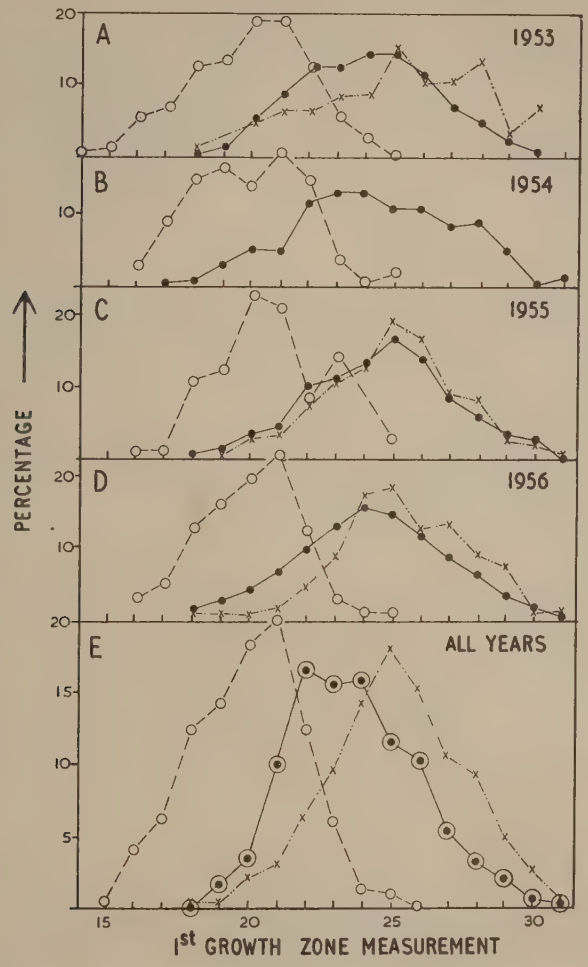


Figure 4. A–D. Frequency distributions of otolith zone measurements in "narrow" type for 3 year-old spawners (×–··–×), all spawners (●——●) and Moray Firth pre-recruits (○–––○). Sample of 3 year-olds in 1954 too small for inclusion in B.
E. Distributions of zone measurements in "narrow" type for 3 year-old spawners (×–··–×), Moray Firth 2 year-old pre-recruits (○–––○) and Bløden 2 year-old pre-recruits (⊙–––⊙), all years combined.

point to the presence of distinct 0-group nursery areas from which the major adolescent pre-recruit concentrations in the Bløden area are derived. By analogy with the origins of "hard" and "soft" scale types identified by Lea (1929) it is probable that the "narrow" zoned type are from a more northerly or colder winter first year nursery area than the "wide" zoned type.

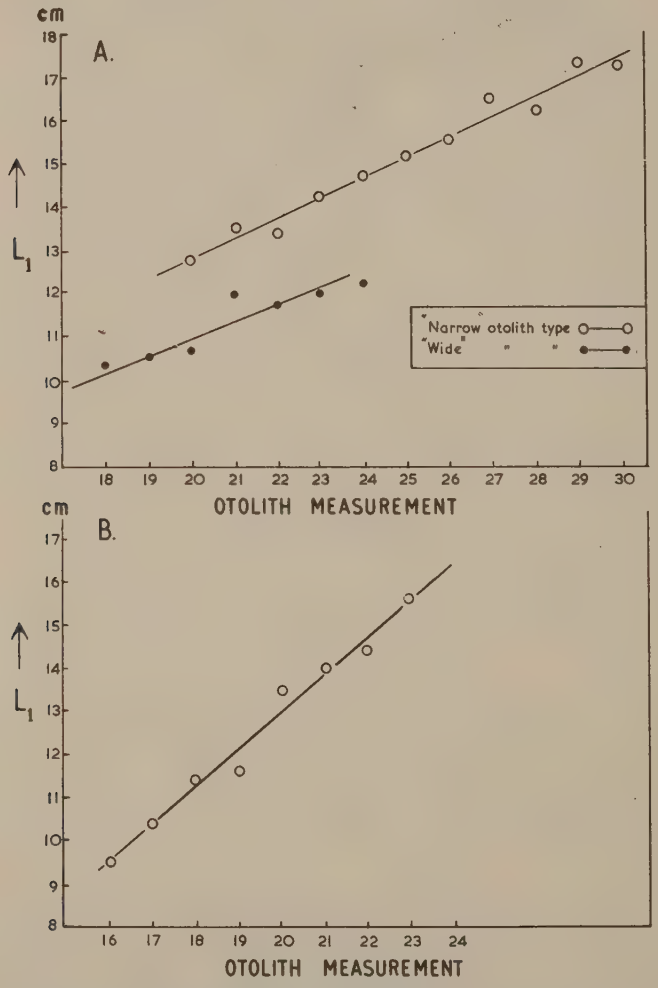


Figure 5. A. Mean L_1's and otolith measurements for "wide" and "narrow" types amongst Scottish east coast spawners (all ages) in 1955.
B. Mean L_1's and otolith measurements for "narrow" type amongst Moray Firth pre-recruits in 1952.

The change in the proportions of "narrow" and "wide" types between ages 3–6 amongst each year-class of spawners might be the result of either an immigration to the Scottish spawning area of fish which had previously spawned elsewhere, or delayed recruitment of the slower growing members of a self-contained stock. With data covering only four years of the life of a year-class in the spawning concentrations it is not possible to establish which of these

Table 5

Ranges and means of L_1 measurements (cm) for Scottish east coast 3 year-old recruit spawners and Moray Firth and Firth of Forth pre-recruits

Year	Scottish east coast recruit spawners		Moray Firth pre-recruits		Firth of Forth pre-recruits	
	Range	Mean	Range	Mean	Range	Mean
1953.....	10–19	15·4	8–18	13·4	–	–
1954.....	11–20	15·2	7–16	11·9	9–18	12·0
1955.....	11–20	15·4	9–17	13·1	8–16	12·1

mechanisms is the operative one. Subsequent data on the older age-groups of the 1951 and 1952 year-classes, which were characterized by low proportions of the "wide" zone type in age-groups 4 and 5, and 4 respectively should provide further important information of relevance to this problem. While the data for age-groups older than 6 do not reveal the same marked change in the proportions of the two otolith types as in the younger age-groups, it is of interest that, in each of the years studied, the proportion of the "narrow" type was higher amongst fish older than 10 years of age than amongst those between 7 and 10. It is amongst these older age-groups that in recent years there has been a marked increase in abundance in the catches of the spawning fishery (Parrish and Craig, 1957).

While the results of this preliminary survey provide some important pointers to the supply and composition of spawners in the north-western North Sea, gaps in the study of the otolith types must be filled before their full biological significance and usefulness in herring "racial" studies can be assessed. The most important of these gaps includes the study of the otolith types amongst the pre-spawning herring in the north-western North Sea, the spawners from other areas, especially the Dogger and Southern Bight, and a wider coverage of the nursery areas, especially the regions to the south of the Dogger and in the Skagerak.

Summary

1. The occurrence of "narrow" and "wide" first winter zones in the otoliths taken from maturity stage VI and VII herring from the Scottish east coast spawning grounds, and amongst pre-recruits from the main nursery areas in the north-western North Sea (Moray Firth and Firth of Forth) and the Bløden area, has been studied over the period 1953–1957.

2. The youngest age-group represented amongst the spawners produced only "narrow" type otoliths, but both types were present amongst all older age-groups. The proportion of the "wide" type increased between ages 3–7.

3. Only the "narrow" type was present amongst pre-recruits from the Moray Firth and Firth of Forth in those years, but both types were present amongst the pre-recruits from the Bløden area. This and the predominance of the "wide" type amongst spawners in the Southern Bight and English Channel suggest that the "wide" type spawners in the Scottish area may have been derived from southern nursery areas.

4. Measurements of the first growth zones of "narrow" type otoliths exhibit marked differences between the recruit spawners and the pre-recruits of the

same year-class from the Moray Firth and Firth of Forth nursery areas, but a close similarity with the "narrow" type pre-recruits from the Bløden area. It appears, therefore, that in the years studied few, if any, of the "narrow" type spawners were recruited from the northern nursery grounds and that they were derived from the more remote nursery areas, possibly also to the south.

5. There is a close linear correlation between the first growth zone measurements and L_1's calculated from scale measurements for both "wide" and "narrow" types.

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Temperature and Growth — The Pacific Razor Clam

By

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Introduction

Quantitative relations between growth parameters of the cod (*Gadus morhua* L.) and mean annual sea surface temperature at various localities have been described by TAYLOR (1958a). This paper shows similar relations for a more sedentary organism, the Pacific razor clam (*Siliqua patula*). The theoretical significance of such relations is discussed briefly.

WEYMOUTH and MCMILLIN (1931) show age-length data for the razor clam at ten localities ranging from California to Alaska. Using these data but excluding median lengths based on less than 5 clams, I have determined the parameters of the equations:—

$$L_{t+1} = mL_t + i \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad \ldots\ldots\ldots\ldots\ldots\ldots (2)$$

and

$$A_{.95} = t_0 + \frac{2{\cdot}996}{K} \quad \ldots\ldots\ldots\ldots\ldots\ldots (3)$$

Equation (1) is the regression of length at time $t + 1$ on length at time t, m being the slope and i the y-intercept (WALFORD, 1946). Equation (2) is the Bertalanffy (1938) growth equation, L_∞ is the asymptotic length, K a constant, and t_0 a correction on the time axis. L_∞ and K are derived from equation (1) as follows:—

$$L_\infty = i/(1 - m) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (4)$$

and

$$K = -\log_e m \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (5)$$

Equation (3) defines the life span as time, $A_{.95}$, required to attain 95% of L_∞ (TAYLOR, 1958a, 1958b).

Table 1 shows the localities and latitudes from which age-length data for the razor clam are reported by WEYMOUTH and MCMILLIN (1931); also the estimated mean air temperature and the parameters K, i, L_∞, and $A_{.95}$.

Table 1

Growth parameters of *Siliqua patula*, California to Alaska, and estimated annual air temperatures

Locality	Latitude N	Estimated mean air temp. °C	K	Growth parameters t (cm)	L_∞ (cm)	$A_{.95}$ (years)
Pismo, California	35°11′	14·4	1·11	8·48	12·72	3·57
Crescent City, Oregon	41°45′	12·2	0·60	6·25	13·87	5·84
Channel (Copalis), Wash...	46°58′	10·3	0·56	5·30	12·34	6·20
Sink (Copalis), Wash.	46°58′	10·3	1·09	7·87	11·84	3·65
Copalis, Washington	46°58′	10·3	0·73	7·24	13·98	5·02
Massett, B. C.	53°20′	8·0	0·47	5·24	14·00	7·26
Controller Bay, Washington	60°00′	5·0	0·16	2·39	16·50	19·60
Karl Bar (Cordova), Alaska	60°27′	4·6	0·21	3·31	17·66	15·17
Swickshak Beach, Alaska..	58°05′	5·9	0·24	3·59	17·02	13·38
Hallo Bay, Alaska	58°50′	5·9	0·22	3·28	16·60	14·53

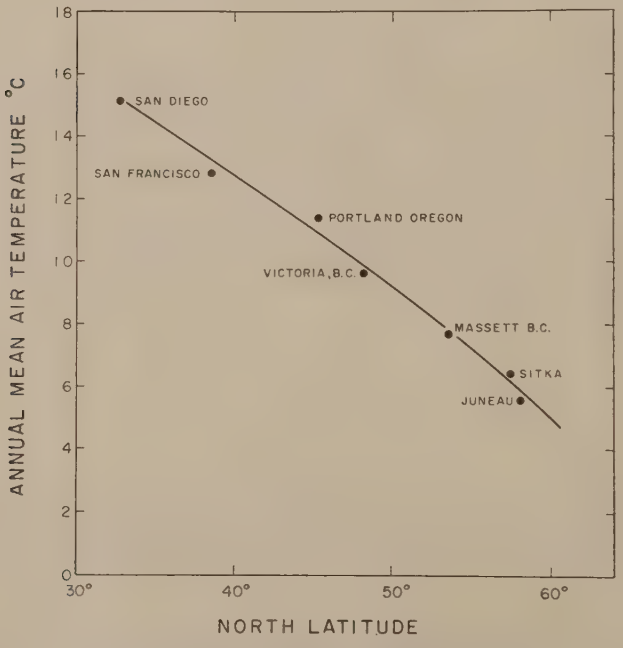

Figure 1. Smoothed curve of air temperature against latitude, San Diego, California to Juneau, Alaska.

Estimation of Air Temperatures

As an index of the thermal environment of the razor clam, I have used mean annual air temperatures at San Diego and San Francisco, California; Portland, Oregon; Victoria and Massett, British Columbia; and Sitka and Juneau, Alaska (CLAYTON, 1927). These temperatures coincide approximately with the period during which WEYMOUTH and MCMILLIN made the growth observations. Razor clams are found in shallow water where the overlying air has a direct influence and the beds are exposed for varying periods at low tide.

Mean annual temperatures were plotted against latitude (Figure 1) and a smoothed line drawn through the points. The mean annual air temperature at the localities listed in Table 1 was estimated by reading temperatures from the smoothed line corresponding to the latitude of each locality.

The three localities at Copalis, Washington are assigned the same temperature. These beds differ in substrate, exposure to wave action, and weather and other characteristics (WEYMOUTH and MCMILLIN, 1931, p. 552). Such factors affect the degree of chilling or warmth and must contribute to the variability of observed relations.

Growth Parameters and Mean Air Temperature

Growth equation (2) is derived from relations which body mass and surface area bear to anabolic and catabolic processes (BERTALANFFY, 1938).

BRODY (1945) shows that the equation (ARRHENIUS, 1889) expressing speeds of reactions in terms of temperatures can be reduced to the form:—

$$S = Ae^{cT} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (6)$$

in which S is the speed of the process at temperature, T (°C), A a constant, and c the differential increase in relative rate of change for 1°C change in temperature.

Taking logarithms of (6):

$$\log_{10} S = \log_{10} A + CT \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (7)$$

where C is now c ($\log_{10} e$). Equation (7) indicates a linear relation of the logarithms of growth parameters to temperature if they are in fact indices of metabolic rates.

Figures 2 and 3 show the logarithms of K and i plotted against temperature for the localities in Table 1. The regression of log K on temperature is:—

$$\log K = 0{\cdot}0849\,T - 1{\cdot}0987 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (8)$$

with correlation coefficient 0·916. The regression of i on temperature is:—

$$\log i = 0{\cdot}0513\,T - 0{\cdot}2430 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (9)$$

with correlation coefficient 0·908. The 1% level of significance for eight degrees of freedom is 0·765.

From equations (8) and (9) one readily calculates that life span and maximum size vary with environmental temperature in a manner similar to that for the cod (TAYLOR, 1958a).

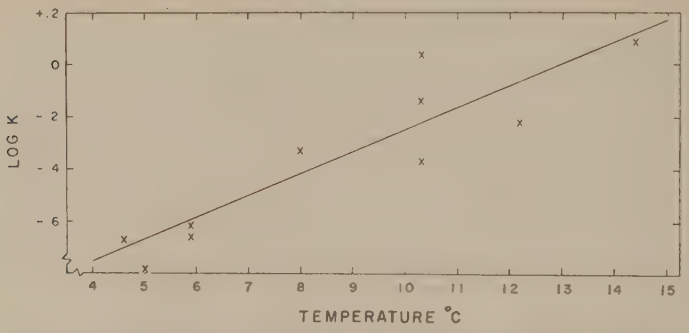

Figure 2. Regression of log K on estimated air temperature for razor clams at the 10 localities shown in Table 1.

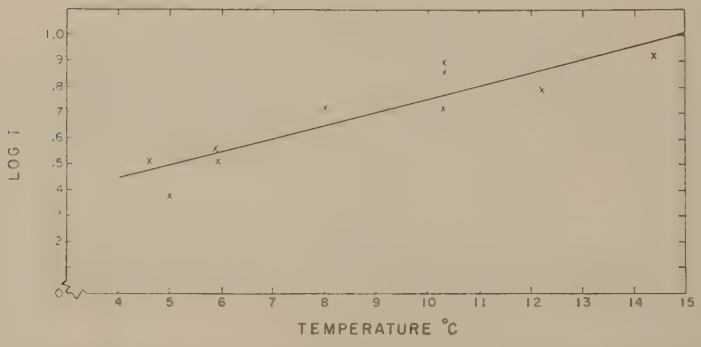

Figure 3. Regression of log i on estimated air temperature for the razor clam at the 10 localities shown in Table 1.

The Relation between E and K

K is a constant related in its derivation to catabolism. E is related to anabolism (BERTALANFFY, 1938) and is of no less interest than K. A more general form of equation (2) is:—

$$L_t = E/K - (E/K - \mathrm{L}_0)\, e^{-Kt} \quad \ldots\ldots\ldots\ldots\ldots \quad (10)$$

Inspection of (10) shows that as t approaches infinity the limiting value of L_t is E/K. We may then estimate E by equating L_∞ to E/K.

Figure 4 shows E plotted against K for the razor clam data. The relation is linear, with regression equation:—

$$E = 11{\cdot}557\, K + 1{\cdot}193 \quad \ldots\ldots\ldots\ldots\ldots \quad (11)$$

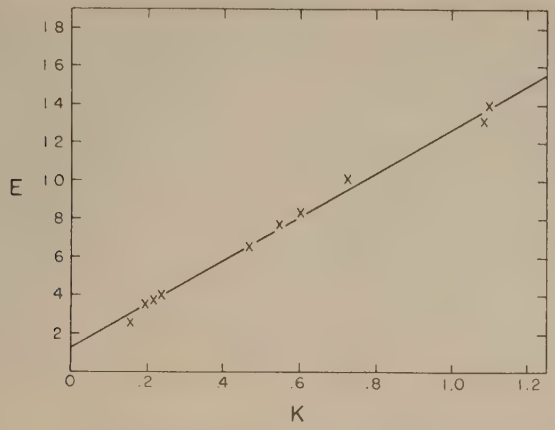

Figure 4. Regression of E on K for the razor clam.

E and K for other Species

Our studies of the published data on the age-length of many fish and shellfish show a species-characteristic linear regression of E on K. These relations hold whether the data represent a wide range of environmental differences in the localities where the species is found or variations occurring in time within a single locality.

Table 2 and Figure 5 show regression lines fitted to E- and K-values for a number of species of fish and shellfish, together with sources of data. These regressions assemble many data for each species, representing growth data from a number of different localities, data for different year-classes in the same locality, or growth data based on back calculations from different ages of capture. The correlation coefficients included in Table 2 merely indicate variability in the goodness of fit. They have no other special significance since E is not estimated independently of K.

Discussion and Evaluation

The quantitative association of growth parameters to temperature for two species, the cod and the razor clam, and the strong probability that such association will be discovered for many other species as adequate temperature data become available, suggests an entirely new group of hypotheses in approaching certain fishery and biological problems. It does not seem premature to explore theoretically a few implications of the growth equations.

Density-dependent growth

Beverton and Holt (1957, pp. 107, 108) cite various references indicating growth is density-dependent, with food the limiting factor. Evidence of this kind is frequently used to explain growth variations as effects of fishing, that

Table 2

Regression equations of E on K for several species of fish and shellfish, together with sources of data, correlation coefficients, and degrees of freedom

Species	Sources of data	Regression slope	Equation intercept	*r*	d. f.
Cisco, *Leucichthys artedi*	STONE (1938) EDDY and CARLANDER (1942b)	22·596	3·904	·953	3
Cockle, *Cardium edule*	COLE (1956)	3·040	0·347	·894	9
Cod, *Gadus morhua*	JENSEN and HANSEN (1931) THOMPSON (1943) GRAHAM (1934) MARTIN (1953)	85·005	6·514	·946	9
Haddock *Melanogrammus aeglefinus*	U.S.F. and W. Service unpublished data	43·154	8·653	·900	13
Kiyi (female) *Leucichthys kiyi*	DEASON and HILE (1947)	24·699	0·620	·997	3
Large-mouthed black bass *Micropterus salmoides*	BENNETT (1937) EDDY and CARLANDER (1942b) BECKMAN (1946)	31·273	4·910	·971	10
Muskellunge, *Esox masquinongy*	SCHLOEMER (1936)	14·994	6·100	·866	8
Perch, *Perca flavescens*	CARLANDER (1950)	17·533	2·700	·995	4
Pygmy whitefish *Corregonus couteri*	ESCHMEYER and BAILEY (1954)	1·876	8·001	·960	9
Razor clam, *Siliqua patula*	WEYMOUTH and MCMILLIN (1931)	11·557	1·193	·950	8
Wall-eyed pike *Stizostedion vitreum*	EDDY and CARLANDER (1942a) SCHLOEMER and LORCH (1942)	29·178	5·516	·901	23

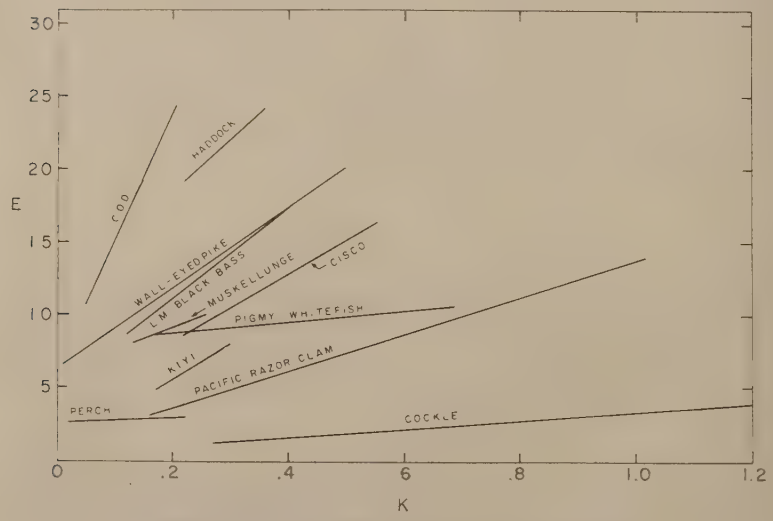

Figure 5. The regression of *E* on *K* for various species. The regression lines are limited to observed values of *K*.

is, the degree of thinning of the stock. BEVERTON and HOLT state (1957, p. 106), "It is possible that different levels of food consumption may result in some change in the general metabolic activity, and thus affect the rate of catabolism as well as that of anabolism, but these changes are likely to be of minor importance compared with the variations in the rate of anabolism that would result directly from the considerable changes in rate of food consumption with which we shall be concerned. From this it would seem that changes in growth resulting from changes in population density are most suitably represented by appropriate changes in the magnitude of the coefficient of anabolism."

The conclusion is contrary to the evidence shown in Table 2. Linearity between E and K between and within environments indicates that in nature, the organism either never gets, or does not take advantage of, excess food. For these species E (anabolism) does not vary independently of K (index of catabolism).

Natural mortality rate

For the shorter life span (equation 3), the *average* natural mortality rate must be higher. This is a simple geometrical principle. On the basis of different rates of growth associated with LEE's phenomenon in haddock (TAYLOR, 1958 b), I postulated different life spans associated with differential natural mortality for each rate of growth. If natural mortality is assumed proportional to numbers present at time t (BEVERTON and HOLT, 1957, p. 29), it becomes a function of K and for two species, at least, a function of environmental temperature. The appropriate estimate for maximum natural mortality for simple population models is:—

$$\frac{N_t}{N_0} = e^{-Mt}$$

where $t = A_{\cdot 95}$, or:

$$M = 2{\cdot}996/A_{\cdot 95}$$

$$\text{or: } M = \frac{2{\cdot}996K}{2{\cdot}996 + Kt_0} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (12)$$

Variations in yield

The importance of the parameter K in the BEVERTON and HOLT (1957) yield equation has been explicitly stated by PARRISH (in press) who notes variations in the yield curve for species with different values of K. The variation of K for a given species with environment or within environment affects yields in precisely the same manner as the between-species variations studied by PARRISH (provided we ignore the possibility of K-dependent natural mortality).

From the relation between K and temperature for cod (TAYLOR, 1958a) I have calculated yield curves for cod over the range 5° to 9°C at fishing rates 0·4 and 0·5, natural mortality rate 0·1, and age of first capture of 4 years. The results (Figure 6) show that the magnitude of temperature changes occurring during the past quarter century in the northern hemisphere could, theoretically, alter yields more substantially than effects attributable to fishing. Certainly changes in age composition and growth-rate not assignable to fishing have been observed (e. g., ROLLEFSEN, 1938).

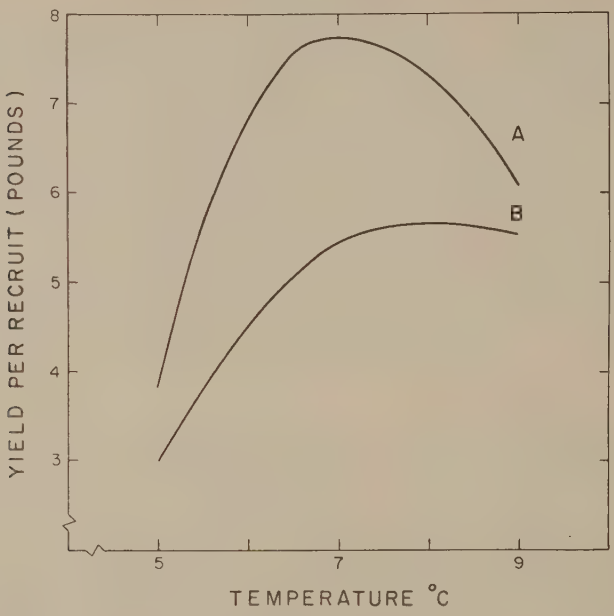

Figure 6. Indicated effect of changes in mean sea surface temperature on cod yields at two levels of fishing intensity (*A*, $F = 0{\cdot}4$; *B*, $F = 0{\cdot}5$) and age of first capture at 4 years.

Summary

Growth parameters of the Pacific razor clam, *Siliqua patula*, are quantitatively associated with mean annual air temperatures at localities ranging from California to Alaska. It is shown that values of E and K follow a species-characteristic linear trend. Theoretical effects on growth, natural mortality, survival, and yield of a fishery are examined.

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Reviews

Hilary B. Moore. "Marine Ecology". John Wiley, New York, 1958. 493 pp., numerous figures.

A comprehensive source book on the ecology of the ocean needs no apologia. As Professor MOORE points out in his introduction, no such work has been available: hence, the present book. Even though there is the valuable treatise on marine ecology and palaeoecology (HEDGPETH, *et al.*, 1957), this book will be welcomed by all marine biologists. It appears at a time when man is beginning to act as though he is a dweller of the universe. Now we have already been told by marine geologists that in many ways we know more about the face of the moon than about the interface between land and sea. Before this becomes even truer, it is good that one practising marine ecologist has found time to write a book on life in the largest living space on the earth. The qualifications needed for such a task cannot reside in a single person, but the author's researches have ranged from estuarine to oceanic ecology. And in writing this book, he has very properly drawn on his experiences and experiments.

The first hundred pages of this book are devoted to an excellent review of the physical and chemical factors of marine environments, factors that are considered in relation to life histories, growth, settlement, behaviour, distribution, flotation, and so forth. Then comes a surprisingly short chapter of some twenty pages on the biological factors, followed by an eighty-page treatment of the various habitats. The remaining 220 pages are given to the organisms themselves. It is clear from the full list of references that this book must have been nearing completion in 1952. Although the author was an early student of deep scattering layers, there is no treatment of recent research. Neither bathyscaphes nor *Pogonophora* appear in the index. However, the book is a lucidly written review of eighty years of marine biology.

The author's approach to his subject is soon made plain. The tendency for marine ecology to separate into studies of single species (autecology) and communities (synecology) is regarded as unfortunate. There is a third aspect "... one that has so far been attempted only rarely but will certainly develop as our knowledge progresses: it might be termed integral ecology. The three parts form a circle, with synecology surveying the broad field, autecology differentiating this into its components, and integral ecology recombining these into the original while". Both approaches have been stimulated by the needs of fisheries research. Fisheries naturalists need no introduction to autecology and for synecology have the classic work of C. G. J. PETERSEN on which to build. More recently, new insights have been provided by G. THORSON's

work on the larval ecology, settlement, and food requirements of the animals belonging to communities in the Danish Sound. Further investigations along these lines, together with others on metabolism, energy flow, behavioural interactions, can be expected to lead to a closer appreciation of integral ecology and ecosystems. As HEDGPETH (1957) has remarked: "The study of communities might be likened to the anatomy of ecology, whereas that of ecosystems, with their attendant complications of populations and energy transfer, would be considered the physiology of ecology". However, to return to autecology, there is still an immense amount to be learned of the lives of the commonest species. How much is really known of the schooling reactions of fishes? Measured by the concepts available, very little.

In a book of this kind the author must range rapidly over a variety of aspects (Dr. MOORE does this with great skill). The organisms thus tend to recede into a background of ecological factors and experiments. But when dealing with the most easily explored marine environment, the intertidal region, the author refers to the STEPHENSON's use of the organisms themselves as indicators of the major divisions of this living space. This is an important advance (we all know how much better are the organisms as oceanographers than ourselves). Now the most remote and least easily investigated oceanic environment is presumably the deep sea. But in spite of the vastness of the waters lying between the temperate zones and the relatively few nets that have been fished, a good case can already be made for using the resident pelagic animals as indicators of the three main divisions of oceanic waters; the surface mixed layer, the thermocline layer or transition zone (ca. 100–1,000 m), and the deeper cold bottom waters. Considering the fish fauna, certain sharks, flying-fishes, tunny-like fishes, etc., are well known to be typical of the surface waters, while numerous (mostly small) luminescent fishes (e. g., stomiatoids and myctophids) are a conspicuous element of the communities found in the transition zone. In the waters below live such predatory groups (all with reduced tissue systems) as the ceratioid angler-fishes, the gulper-eels (*Lyomeri*) and monognathid fishes. Perhaps the biological and physical differences between these three subdivisions are so trenchant (particularly in food, temperature and light conditions) that the correlated vertical structure of the animal populations is fairly readily revealed. Furthermore, the mid-waters of the ocean are in some ways a less complex environment than the intertidal regions. While it is early yet to begin to understand "comparative" marine ecology, Dr. MOORE's book will surely stimulate such comparisons. As he concludes: "The science has, in some of its aspects, suffered from the over-collection of data to the point where the mass of material tends to become indigestible. One of the present urgent needs is that there be, along with investigations in the vast field of exploration which is obviously open, more reviewing and co-ordinating of the present information. This has been attempted here from the special point of view of the needs of a student in the field. It is to be hoped that more workers will produce critical reviews of their own specialized fields in marine ecology." The reviewer also shares this hope.

N. B. Marshall

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HEDGPETH, J. W., *et al.*, 1957. "Treatise on marine ecology and palaeoecology". Mem. Geol. Soc. America, **67** (1): Ecology, 1296 pp.

Morski Instytut Rybacki — Gdynia (A. Klimaj St. Rutkowicz). "Atlas Rybachi Morza Polnocnego", (Fishing Atlas of the North Sea), Panstwowe Przedsiebiorstwo Wydawnictw Kartograficznych, 37 charts. Warsaw, 1957.

This publication represents a new dimension in atlases. This one volume contains charted summaries of fishery data and analyses of some of the basic environmental factors related to the fish populations in the North Sea and selected aids to navigation. The task of abstracting, compiling, and integrating information from the thousands of published technical and scientific papers produced on such a major fishing region could probably require a decade of concentrated work by several specialists. This atlas appears to have been done in about 2 years (1955–57); a commendable accomplishment in view of the limited staff that seems to have been devoted to this work.

It is obvious that this atlas has been designed expressly to suit the fisherman-mariner user. The information has been intelligently tailored with careful discrimination applied in the selection of environmental topics for inclusion; the use of colours and simple symbols permits easy reading and understanding of the charts; the presentation of related topics, appropriately treated on the same chart, contributes to the overall usefulness and convenience of the charts; the chart analysis is considered accurate for a "general" presentation; the omission of technical details or scientific refinements which have little operational use have been wisely avoided. Each chart is supplemented with approximately one page of explanatory text, given in three languages, Polish, English, and Russian. The text is well written; good basic general information is presented in readable, non-technical language which should be easily understood by the fisherman-mariner. Valuable supplementary details are included in the text and recognition is made of the primary authorities which provided reference source material.

The atlas is introduced with a brief explanatory note and two general charts of the North Sea. Both charts subdivide the sea into sections or regions. One chart shows the outline of general areas as defined for statistical research purposes by two major international organizations for sea exploration. The second outlines the "fishing grounds" designating each with the conventional name used by local fishermen and mariners. Colours are used to describe the relative degree of importance of each area for fishing exploitation.

The atlas has been divided into two parts, a "General" section and an "Operational" section. The first contains 12 charts which primarily cover selected marine environmental subjects related to commercial fishing; the second contains 24 charts which summarize the relative catch by two different fishing methods and the relative productivity characteristics of two commercial species.

In part I, bathymetry and bottom sediments are shown on separate charts even though the detail does not warrant it. Several physical oceanographic elements are presented; usually related items appear on the same charts. Information is included on tides, currents, and surface temperature. Bottom temperature and salinity information are charted with migration and feeding information. Three fishery charts complete the first section; the first two depict the spawning grounds for several local species of herring and mackerel, the last indicates the best exploitation periods for each area.

Part II on operations provides a series of monthly charts for two types of commercial fishing, trawler and lugger. Each chart shows by size and type of symbols and by colour the kind of fish, the mean catch per day in four weight (tonnage) categories, and the ratio of the total catch by three maturity classes.

The size of the atlas (approximately 12″ × 16½″) is most convenient for desk use; it is nicely bound in a hard permanent book-type cover which should be serviceable for the hard continuous usage required in the fishing industry. However, the chart paper used is not the best for an atlas intended for constant marine use; its high wood pulp content tends to make it absorbent to moisture. All charts are lithographed in multicolour; this not only gives the charts more "eye appeal," but also allows the presentation of related features on the same chart.

In summary, this volume appears to be an excellent compilation and presentation, well planned for the user. It could also serve as a useful reference tool to the beginning student in marine biology and fishery resources; its value to the fishery research specialist seems to be limited and questionable because of the general treatment followed throughout. It is somewhat surprising that such an atlas was not produced earlier by some nation which has a larger fishing industry and which has been (or is) more prominently associated with investigation of fishery problems and applied research than has Poland. Poland has never been considered a major contributor to the world literature on biological oceanography, but the calibre of this publication indicates that fishery research work is on the increase. Accordingly the scientific world can expect a significant increase in technical marine biological papers from scientists of that country in the next decade.

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* The opinions contained in this review are not to be construed as being officially endorsed by the U. S. Navy or Department of Defense.

H. Barnes. "Apparatus and methods of oceanography. Part I. Chemical". George Allen & Unwin, London, 1959. 341 pp.

The analyst plays a vital part in the advancement of diverse branches of science, not least in oceanography, and this fact is not always accorded due recognition. Not a few who find use for the results of analysis are forgetful of the hours or perhaps days of meticulous and skilful work which have gone to the making of an apparently unremarkable list of numbers. Perhaps the reason for this rather common lack of appreciation is to be sought in the fact that the numbers in the list do not at first sight betray the craftsmanship, or lack of it, which has gone to their making, and much therefore depends on the integrity as well as the skill of the analyst. Since reliable analyses are indispensable to progress, it is of the greatest importance that analytical text-books should contain the best advice that experience can offer. Dr. BARNES, himself an authority, has nevertheless taken the precaution of inviting the criticisms of many well known chemical oceanographers. We can therefore expect that this work will be a sound and valuable statement of present knowledge, and this expectation is fulfilled.

Two-thirds of the book are occupied by what may be termed the bread-and-butter activities of the water analyst. This section includes excellent treatments

of the determination of such variables as chlorinity, pH, the various forms of combined inorganic and organic nitrogen and phosphorus, silicon, oxygen, and alkalinity with a concise consideration of the carbon dioxide bicarbonate equilibrium. All these are discussed with an enviable facility, and little more could be required of a working manual.

The opening chapter, devoted to a consideration of colour comparators and photometric analysis, savours somewhat of the manufacturers catalogue in its descriptions of the various forms of photometric apparatus. Perhaps a little too much space is given to descriptions of out of date instruments, one imagines that most workers will now have access to a spectrophotometer and will therefore have a somewhat reduced interest in comparators of lesser precision. However, the section on photometric analysis in general terms is a valuable contribution. The confusing array of unit terms used in photometry is indicated but the confusion is not appreciably resolved. A discussion on the statistical statement of precision will be welcomed by many, though the associated section concerned with errors arising in volumetric analysis (much after E. J. CONWAY) will have a more limited application, possibly confined to the estimation of chlorinity in which a most remarkable standard of precision is obtained with what seems at first sight to be a somewhat archaic procedure.

The theory and practice of electrometric pH determination is clearly and precisely described, with much valuable discussion of the many possible errors associated with the glass electrode. This chapter will provide, perhaps, a timely caution for those whose faith in the pH meter is derived from a scanty understanding of the processes involved.

The chapter on the determination of dissolved and suspended organic carbon and the later section on the carbon content of sediments, would have derived benefit from some mention of the empty tube combustion techniques of BELCHER and INGRAM which are rapidly being accepted as standard methods in the micro-determination of carbon in other fields, and which can provide a rapid and accurate measure of carbon in solids such as plankton and mud. Though the methods available for the determination of dissolved organic carbon are adequately described, one is left with the feeling that much yet remains to be done before a satisfactory routine method for this determination is achieved either in sea water or fresh water. It should also be noted that the determination of total dissolved organic carbon is in itself merely the gateway to a large field of exploration on the nature and function of the individual compounds, a field untouched in this book and scarcely entered upon elsewhere.

The treatment of such elements as sodium, potassium, calcium, and magnesium is sound and rather orthodox. It is surprising, however, to find no reference to the determination of calcium and magnesium by the very valuable complexometric techniques originated by SCHWARZENBACH and his colleagues.

The latter third of the book is devoted to trace metals, plankton pigments, filtration, and the physical and chemical examination of sediments, followed by an appendix of recent literature and a most valuable collection of data in the form of tables. The treatment of the trace metals is brief and is largely confined to work on iron, manganese, and copper. Many will feel that more space could profitably have been given to this subject, which must surely be one of the growing points of chemical oceanography. The examination of sediments is concerned in the main with the purely physical property of particle size distribution, chemistry being confined to a rather brief description of methods of

determination of calcium carbonate and organic carbon. The sediments contain a great deal more than this.

Doubtless a number of volumes would be required to cover adequately the whole field of chemical oceanography, nevertheless this book will interest and stimulate all those concerned in the analysis of waters, fresh or salt, or of the sediments and suspended materials associated with them. It contains a wealth of information, much of which is clearly derived from the author's own experience, and his personal asides add much to the plain description of an analytical method.

F. J. H. Mackereth